The Big Tree of Tule (*Taxodium mucronatum*). This tree, growing near the city of Mexico, has a trunk 50 feet in diameter. It is believed to be the oldest living thing on the earth. (From a photograph by Dr. Charles J Chamberlain.)

Plant Life

A Textbook of Botany

By

D. B. SWINGLE

*Late Dean of the Division of Science
and Professor of Bacteriology
Montana State College.*

SECOND EDITION, FOURTH PRINTING

D. VAN NOSTRAND COMPANY, Inc.

TORONTO NEW YORK LONDON

NEW YORK
D. Van Nostrand Company, Inc., 250 Fourth Avenue, New York 3
TORONTO
D. Van Nostrand Company (Canada), Ltd., 228 Bloor Street, Toronto 8
LONDON
Macmillan & Company, Ltd., St. Martin's Street, London, W.C. 2

First Published, January, 1935
Second Printing, January, 1938

Second Edition, March, 1942
Reprinted February, 1947; February, 1948
December, 1948

PRINTED IN U. S. A.

To the many naturalists

who, since the dawn of civilization,
have seen plants as living individuals,
not as dull objects to be passed by
without notice.

PREFACE TO THE SECOND EDITION

The success of the first edition of *Plant Life* has encouraged the author to continue its publication in slightly revised form. The plan of treating plants as living things, with emphasis on their physiology and behavior, has been a happy one, greatly increasing student interest, and follows modern ideas for presenting a new subject to those not yet familiar with its objectives.

Without sacrificing the technical material which is the foundation of the science of botany, the second edition introduces a little more natural history than was found in the first. This has been done in response to the student interest shown in that feature of the book.

The length of the book has not been greatly changed, the intent being to make it ample for a one semester course. However, in almost every chapter portions that were treated too briefly for clearness have been somewhat amplified. A few new illustrations have been added and better substitutes have been found for others.

With regard to the length of the course in general botany most suitable to the needs of an institution, there is much difference of opinion. Some prefer to offer a full year. Others find it better to cover the subject in one quarter or one semester and offer additional courses in such branches of botany as the students require. However, in institutions that offer general botany as a full year's course, it too often happens that the curriculum of many students calls for only one semester or one quarter of botany. They get the first part of the subject in more detail than they can afford and miss the last part entirely. For them a briefer book such as *Plant Life* has an advantage.

The student who has mastered this book is well prepared to take up any advanced course in botany, or, if he does not plan to do so, he has gained from this study a considerable familiarity with the plant kingdom.

The author wishes to express to Dr. W. E. Booth of Montana State College his grateful appreciation for assistance given in this revision, and for a number of valuable suggestions based on a critical reading of the first edition.

D. B. Swingle.

Bozeman, Montana,
January, 1942.

PREFACE TO THE FIRST EDITION

The student will find the subject of botany presented in this book in a somewhat different way from that commonly used. The prevailing tendency is for a morphological approach, the consideration of function being incidental. The result is that students find their textbooks heavy and dull, and they get little comfort from the fact that trained botanists see them teeming with interest.

In this text an advance is attempted in the method of presentation. Use is made of the fact that our interest in plants and animals centers around life processes—methods of obtaining and utilizing food, methods of avoiding the dangers that beset them on every hand, and the ways by which they are perpetuated through endless generations. Activities in which the plant participates constitute the central theme, and structures are described as mechanisms by which these activities can be carried out. Interest in morphology is thereby stimulated, as the significance of the organs is more fully appreciated. By studying plants in this way the student gets a far better insight into their lives than is ordinarily obtained in a beginning course.

Where possible, use is made of the well-known principle of first arousing a scientific curiosity and then satisfying it, and the student thus makes the natural approach to each new idea that he is to receive. Logical sequence is followed in the main, but at times it is subordinated to the important consideration of satisfying at the critical moment a need for specific information arising in the mind of the student.

Often it has been found expedient and effective to introduce a topic, discuss it in a general way only, and later return to it for a deeper discussion after the student's progress has made him more able to understand it and more ready to appreciate it. Processes of absorption, processes of reproduction, cytological studies, and the structure of roots, stems, leaves, flowers, and fruits are examples of such treatment. For a reference book there are undoubted advantages in having assembled in one place the full treatment of each topic, but in a textbook this is not so important, and the purposes of the author may be defeated by trying to force something upon a student before he is ready to receive it.

Hardness is not in itself an asset to a textbook. Instead the student

should be made to feel that he is not being forced into the subject beyond his capacity or preparation. In the end, it is likely that he will have mastered even more of fundamental botany than he would have done if he had used a more difficult text in which he had only a forced interest and had passed over portions that he could not readily understand. Technical terms are not introduced until there is a need for them, after which they are repeated until they become familiar; and care has been taken to bring in only as many necessary ones as can be mastered in a course of one semester. In the first fifteen chapters, scientific names of plants have been purposely avoided; for until they have been explained, as is done in Chapter XVI, they are apt to discourage the student rather than to stimulate him to adopt them.

The length of a textbook is an important consideration. This book is written to fill a need—the need of the college that covers the field of general botany in one semester. Most of our best textbooks on this subject contain material for a year's work. To adapt them to the time limits of a semester is difficult and unsatisfactory. If entire chapters are omitted, serious gaps are left in the student's fundamental training. If certain paragraphs are omitted from each chapter the assignment is awkward, and incoherence is inevitable.

The author has endeavored to produce a book that contains all the essentials of a first course in botany and that carries out the ideas stated above.

The author desires to express here his indebtedness to his associate Dr. F. B. Cotner, professor of botany, to Dr. O. E. Sheppard, professor of chemistry, and to Dr. A. J. M. Johnson, professor of physics, all of the Montana State College.

Illustrations of exceptional merit have been borrowed where original ones could not be supplied. For permission to reproduce these grateful acknowledgment is hereby given.

D. B. SWINGLE.

January, 1935.

CONTENTS

PART FOUR—THE GROWTH OF PLANTS

INTRODUCTION

Man has always lived with plants. The earth was covered with them before he appeared. With increasing intelligence and experience he made more and more use of them; at first for food, shelter, and weapons, later for clothing, ornament, medicine, boats, bridges, and the myriad of purposes known to modern civilization. Indeed, the extent to which plants were used and the variety of uses to which they were put are a fair criterion of the advancement of civilization among early peoples.

Long before books were written the more progressive tribes cultivated the soil and selected and improved plants in addition to naming them. They were practical botanists although they did not know it.

Origin of Botanical Science.—Our scientific study of plants, based on a desire to know more about them for the sake of knowing, is more recent and began with the Greek philosophers. The Chinese and other early civilized peoples made considerable advancement in a knowledge of plants, but their studies were wholly detached and had no connection with the progress of botanical science in our western civilization. Furthermore, the pre-Grecian botany was more of an art than a science.

The Greek botanists were not experimenters with plants. They observed, exchanged ideas with their neighbors, philosophized, and recorded their conclusions. Often their reasoning was based on insufficient evidence. Nevertheless the books about plants written by Theophrastus, pupil of Aristotle, contain much sound information.

Early Medical Botany.—Wholly apart from the botanical philosophy of Aristotle and Theophrastus, some of the Greeks, notably Hippocrates, found that certain plants had real medicinal value based on their physiological effects upon the human system. This was a great step in advance, for previous to that time the use of plants for medicine had been on a wholly different basis—that of superstition, in which various plants entered into the practices and ceremonies for placating the hostility of evil spirits or obtaining the favor of benign ones. So great was the interest in medicinal plants among the Greeks that this aspect of botany finally eclipsed all others. It was a large factor in the turning of medical practice away from superstition toward treatment

based on observation and experiment. Firmly grounded beliefs, however, are not easily dislodged, and even as late as the sixteenth century the appearance of plants was supposed to indicate their medicinal value. Thus, for example, heart-shaped leaves were used for heart troubles, and kidney-shaped seeds were likewise used for kidney troubles.

FIG. 1. Theophrastus (382 to 287 B.C.). Greatest Greek botanist and writer on this subject. (From Hort's *Theophrastus*, G. P. Putnam's Sons.)

Systematic Botany.—Through the dark ages botany languished as did other branches of learning. In the sixteenth century it was revived and pushed with vigor throughout central Europe in an effort to duplicate the medical skill of the Greeks and to find the plants used by them for healing. With the rise of universities the professor of botany and the professor of medicine became one and the same individual. In some cases he was a better botanist than he was a doctor, and often he collected and named plants with no concern as to their medicinal value.

There was at that time no uniform system for naming plants, and chaos was the inevitable result. Most conspicuous among those who

contributed to good usage in nomenclature was Linnaeus, a Swedish botanist who traveled and worked throughout western and central Europe. Following the example of Bauhin, a Swiss botanist, he adopted and widely advocated the use of the binomial system of Latin names—a generic name and a specific name for each kind of plant—the system which we follow today. In this system the generic name is a noun, often descriptive, followed by a specific name which is a descriptive adjective. This simple method of using two descriptive terms instead of a long series of them, as had previously been done, has found general favor. Since the time of Linnaeus steady progress has been made in the naming and classifying of plants.

In America this branch of botany, stimulated by the inspiring and lovable Asa Gray of Harvard University, was followed for years almost to the exclusion of other botanical studies. The result was a misconception of the very nature of botanical science, and this misconception, that botany is merely the naming of plants, persists in the minds of many American people to this day.

Evolution.—In the days of Linnaeus, when systematic botany was in the making, it was generally assumed that the species of plants and animals were unchanging. It is true that several workers had arrived independently at the conclusion that one species may come from another, but their brief statements were unnoticed.

In the middle of the nineteenth century Charles Darwin and Alfred R. Wallace, two English botanists, independently arrived at the conclusion that new species have arisen by progressive changes in older ones. When Darwin published his book, *Origin of Species,* his forceful presentation of the evolutionary conception drew world-wide attention. Had this method of origin been applicable to plants and lower animals only, it might have been received with universal favor, but unfortunately man in his pride and egotism took offense at that portion of the theory that referred to his ancestry, and, being more sentimental than scientific, sought to crush it under a weight of argument. Indeed, many lost sight of the fact that this method of origin by evolution is a general one, applying to hundreds of thousands of species of which man is only one. Others accepted the idea and struggled, with varying success, to learn in detail the evolutionary steps that have taken place and the causes of the variations whereby offspring differ from their parents. At the present time systems of classification are universally based on efforts to trace in plant and animal groups actual relationships resulting from a common ancestry.

The Internal Structure of Plants.—The early botanists could study plant anatomy only in a very general way, for they had no microscopes. They were especially handicapped in their efforts to study the tiny lower plants. The compound microscope was invented by J. and Z. Janssen in 1590, but it was so crude that for a century or more few people were able to use it effectively.

Late in the seventeenth century an English scientist, Robert Hooke, with a bent for mechanical work, made considerable improvement on the microscope and set out to convince the world of its value. Among other things he examined thin slices of cork obtained from the bark of a tree and found it to be made up of little boxes which he called *cells*. He compared the structure of cork to that of a honey-comb and estimated that there must be one billion two hundred million of these cells to a cubic inch of cork. The cork cells were dry and empty, having lost their living contents with age. However, he observed sap in the cells of some living plants although he did not comprehend its significance as living *protoplasm*. His work was published in 1667.

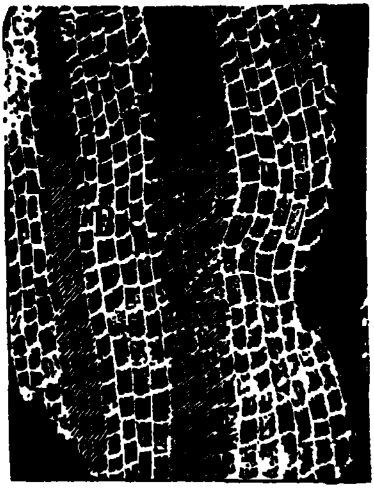


FIG. 2. Cell walls of cork as discovered and drawn by Robert Hooke in 1665. (From Smith, Overton, et al., *Textbook of General Botany*, The Macmillan Company.)

Shortly after Hooke's discovery another Englishman, Nehemiah Grew, and an Italian physician, Marcello Malpighi, simultaneously published illustrated works, quite remarkable for their time, on the internal structure of many plants. Thus the mechanical genius of Hooke, the industry and painstaking accuracy of Malpighi, and the enthusiasm and vision of Grew opened a great new field for investigation on the anatomy of plants. It must be understood, however, that their conception was quite different from that of today. They thought of the plant as a unit, subdivided by many tiny partitions or cell walls. We think of the individual cells as living protoplasmic units bounded by walls, and the aggregate of cells as making up the

plant. Later discoveries of the cell protoplasm with its nuclei and other parts diverted attention from the cell walls to the more significant cell contents.

In all branches of learning little detailed discoveries are made, the significance of which is not fully realized, and later a genius appears who, with greater vision, constructs of these fragments a usable theory or law. Thus two Germans, Schleiden, a botanist, and Schwann, a zoologist, working in conference in 1838 constructed the cell theory—that all plants and animals are collections of cellular protoplasmic units. At a slightly earlier date a French botanist, Dutrochet, had arrived at this conclusion, but, as so often happens, his published statement, significant as it was, escaped attention and had no influence on subsequent work. Later studies in this field, with microscopes superior to anything dreamed of by Schleiden and Schwann, have wholly revolutionized the study of botany.

Studies in Plant Physiology.—To know what plants look like is worth while, but to know how they live, what they do, and how they do it is vastly more significant. This is plant physiology. The ancients were fairly good observers but not experimenters. The simplest experiments, the joy of every modern schoolboy, were not even thought of by the Greek philosophers. Therefore they made little progress in this field, and most of their speculations were misleading. Physiology centers largely around the processes of nutrition, growth, and reproduction, and the various expressions of the condition known as *irritability*. It has been known for a very long time that plants obtain water and food materials [1] from the soil, but the discovery that green plants obtain a large part of their food materials from the air under the influence of light and that this is the most important method of taking energy from the sun is comparatively recent. Again, this discovery was not made in a single stroke by one man. One pertinent fact after another was brought to light by different workers, and in 1804 a French chemist, De Saussure, brought these ideas together, added to them, and summarized the whole situation thus: "My researches have enabled me to

[1] In relation to plant nutrition the word "food" is used by different authorities in two different ways. (1) A food may be any substance that enters into the composition of the plant—water, mineral salts, carbon dioxide, carbohydrates, etc. (2) It may be restricted to those organic substances that can yield energy by oxidation—carbohydrates, fats, proteins, etc.; but not water or minerals, these inorganic materials and carbon dioxide being classed as "food materials." This second usage will be followed in this book.

demonstrate how much greater is the contribution of water and air to the formation of the dry material of plants growing in fertile soil than the materials which they absorb in the water through their roots."

Early studies in plant reproduction were rather superficial. Aristotle maintained, without evidence, that pollination of flowers served a nutritional purpose. The whole subject of reproduction in plants was hopelessly controversial until near the close of the seventeenth century when a German botanist, Camerarius, performed actual experiments that showed the necessity of pollination for seed production and stimulated other experiments in this field. These led to the development of the great subject of genetics, which deals with inheritance in plants and animals.

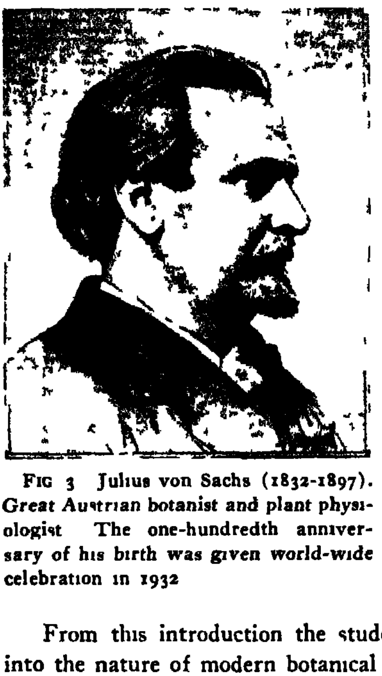


FIG 3 Julius von Sachs (1832-1897). Great Austrian botanist and plant physiologist The one-hundredth anniversary of his birth was given world-wide celebration in 1932

The great Austrian botanist, Julius von Sachs, did more, perhaps, than any other man to weld the scattered fragments into a science of plant physiology. The hundredth anniversary of his birth was widely celebrated in 1932.

From this introduction the student will have gained some insight into the nature of modern botanical studies, which are but a continuation and improvement of the cruder pioneer observations.

Review Questions

At the close of each chapter a set of review questions is given. The student should be able to answer all of those pertaining to one chapter before going on to the next As a rule the answers can be found in the text of that chapter, but purposely a few questions are asked that call for wider reading.

1. Name three things that uncivilized man did with plants that might be classed as primitive botany.

2. In what countries did botanical studies make material progress before the beginning of the Christian era?
3. Which of these studies survived to form a basis for the botanical learning of today?
4. How were plants first used in medicine?
5. What different use did Hippocrates and other Greeks make of plants in medicine?
6. What branches of botany received attention during the early development of European civilization?
7. Name two pioneer workers who helped to found each of the following branches of botany: (1) medical botany, (2) systematic naming of plants, (3) studies in evolution, (4) internal structure of plants, (5) plant physiology.
8. Give the nationality of each of these pioneer workers.
9. Why was a knowledge of the *minute* structure of plants impossible for ancients to acquire?
10. How and by whom were cells first discovered?
11. How much of the cell was seen by him?
12. Define: (1) morphology, (2) physiology, (3) cytology.
13. What nation produced men more inspired than earlier peoples to learn for the sake of knowing as well as for economic purposes?
14. Of the six topics discussed in this introductory chapter, which ones do you think could be appropriately used in an introduction to the study of animals?

PART ONE

THE LIVING PLANT

CHAPTER I

PLANTS AS WE SEE THEM

Man's greatest heritage is the wealth of vegetation that covers the earth. There are few more enchanting sights than the great expanses of grass, the fields of flowers, and the majestic forests that adorn our landscapes. In a large measure plants furnish us with food, clothing, and shelter, with medicines, with chemicals, and with unsurpassed materials for decoration. The science of botany has aided in the development of some of our greatest industries—agriculture, forestry, textiles, etc.

Collectively plants furnish us with inspiring fields for contemplation, but to understand and appreciate them we must investigate them as individuals. We must realize that there are on the earth thousands of plant species differing as widely as do the mushroom and the rose.

A Representative Sample

A good example of our flowering plants is the sunflower. Starting from the seed, it extends its roots downward and outward into the soil and its stem and branches upward and outward into the air. It is a thing of life, taking up food materials, growing, and reproducing its kind. It even moves its showy head in response to the stimulus of light from the sun. To understand such a plant fully—its parts and their behavior—is to understand much that applies to plants in general.

What appeals to the eye is the graceful form and the striking colors. A study of these characters, the size, shape, color, etc., we call *morphology*. On this basis we recognize three distinct parts to the body of the plant, the *root* with its branches, the *stem* with its branches, and the *leaves*. Specialized stems and leaves make up the various parts of flowers and fruits. As a living individual the plant has life problems as interesting and as complicated as those of animals. How shall it remain in place, resisting winds, storms, and floods? How shall it utilize

the energy from the sun? How shall it obtain its food and grow? How shall it reproduce and get its seeds distributed over the earth? How shall it be protected from inclement weather and the depredations of animals and disease? By devices most intricate and effective these problems are solved. The plant is provided with organs especially suited to its needs and these will here be introduced. Plants, like animals, have many kinds of work to do, many functions, and the highly specialized organs make possible an effective division of labor.

FIG. 4. Small sunflower plant showing branching stem with its nodes and internodes, simple leaves, and large head of small flowers.

Three Main Parts of a Flowering Plant.—Anchorage to the soil is accomplished by the root system, often of great strength and intricately branched. The roots serve a double purpose, however; they not only anchor the plant but they absorb food materials and water from the soil. A third function of roots is food storage, although the roots of the sunflower and of many other plants are not highly developed in this respect.

The body of the plant is largely made up of the stem with its branches. At definite intervals on the stem leaves are produced. These leaf-bearing regions are called *nodes* and the stretches between them are the *internodes*.

The leaves of a sunflower have easily recognizable parts. The broad expanded portion is the *blade* and the stalk that attaches it to the stem is the *petiole*. The leaves of some other plants have also a pair of small green scales at the base. These are called *stipules*, but their function is not usually evident. Sunflowers and many other plants do not have them, while on still other kinds they are produced but fall off very soon. The *veins* of the leaf are very conspicuous. There is a central *midrib*

running through the middle line from the base to the tip. From this midrib branches run out to the margins and divide into smaller veins that intersect each other in a sort of network. Such *venation* is termed *netted*. These veins carry water and food materials through the leaf.

At the top of the stem and at the tips of the larger branches are conspicuous heads of flowers. The careless observer looks upon each of

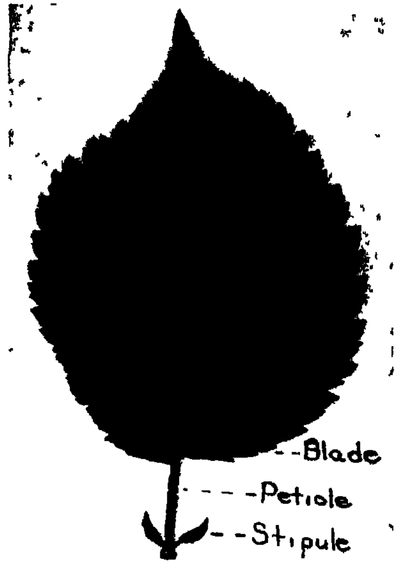


FIG. 5. Young leaf of apple illustrating all parts—blade, petiole, and stipules.

these as an individual flower, but the student will soon discover that each is a flower cluster or *inflorescence*. There is a border of conspicuous yellow *ray* flowers surrounding a dark center of small *tube* flowers.

Length of Life.—Plants like the sunflower, that attain their full development in a single season and die in the autumn after producing seeds, are called *annuals*. *Biennials*, on the other hand, do not produce seeds until the close of the second season, after which they die. Cabbage, beet, and carrot are examples. *Perennials* live on indefinitely, usually producing seeds each year. They are illustrated by peony, columbine, lilac, and rose. Whether a plant is annual, biennial, or perennial is determined by the length of life of the underground portion—root, stem,

or both. The aerial portion of the stem of many plants dies to the ground in the fall while the root and the basal portion of the stem live on for a year or more longer, sending up new stems in the spring. Plants are called *herbaceous* if their stems die to the ground each year and new succulent ones grow up the next season. If the stem lives for years and becomes hard and tough the plant is classed as *woody*—a tree, a shrub, or a woody vine. Trees are relatively large, with a single trunk, while shrubs or "bushes" are smaller, with many main stems. Some species of trees are very long-lived, notably the big trees of California and the bald cypress. A Montezuma cypress, the "Big Tree of Tule," near Mexico City is estimated to be about five thousand years old. It is doubtful if any living thing on the earth is older. (See frontispiece.)

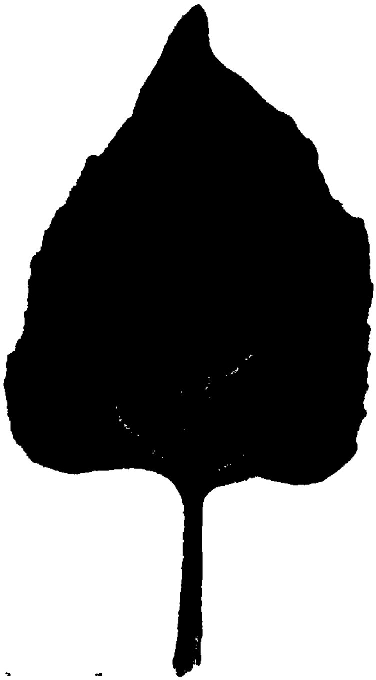


FIG. 6. Leaf of sunflower with netted-veined leaves typical of dicotyledons.

ENDLESS VARIETY IN PLANTS

The sunflower is an excellent type of plant for general study and much can be learned from it. It is well, however, to broaden our working knowledge of the common plants about us by further observations on representative species. To this end a half dozen others will be given a brief description, each chosen to illustrate one or more useful points in botany.

Red Clover.—This plant, so common in fields and along roadsides, differs from the sunflower in several respects. It is a biennial or triennial, i.e., it produces no flowers and seeds the season it is planted, but it does reproduce the second season and usually the third. When full grown it has a strong, deep root system and a stem that branches

close to the ground. The leaves are especially worthy of notice. Each has three parts to the blade—three *leaflets*. It is, therefore, a *compound* leaf. In the compound leaf of clover, horse-chestnut, and lupine the leaflets are all attached at one point on the end of the petiole. Such a leaf is *palmately* compound. In this plant, as in the sunflower, the leaves have netted veins. Red clover is a favorable plant for the study of stipules, for they are very conspicuous at the base of each leaf. The head of clover is very different from that of the sunflower. The flowers in it are all alike in color and shape, there being no ray flowers. Careful study reveals that this inflorescence is more like a very short, broad spike or raceme than a head. (See page 170.)

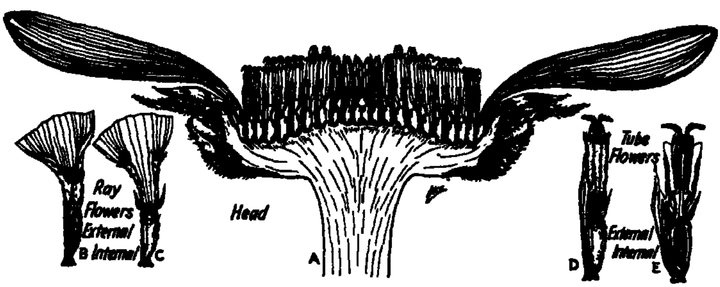


FIG. 7. Longitudinal section of sunflower head, showing ray flowers at the margins and tube flowers in the center.

Easter Lily.—Among the numerous lilies the Easter lily is here selected as one of the best known, since it is extensively grown in greenhouses and sold by florists. The plants are propagated by bulbs, each bulb consisting of a compact mass of thick leaf bases attached to a very short stem. When this stem grows up to bear flowers it is usually unbranched and produces leaves without petioles. Such leaves are called *sessile*. Usually there is only one at a node, but some other lilies produce several at each node. Such an arrangement of leaves in groups of three or more at a node is *whorled*. An important difference between the leaves of this plant and those of the sunflower is that in the lily leaves the main veins are *parallel* and *unbranched*. The flowers of the Easter lily are large and showy, but there are few on a stem, sometimes only one or two.

Corn or Maize.—The stem of this annual plant has very conspicuous nodes at each of which one leaf is attached to the stem all around by a basal leaf *sheath*. The leaves of corn, like those of the lily and the

FIG. 8. Red clover plant with compound leaves and tiny flowers in heads.

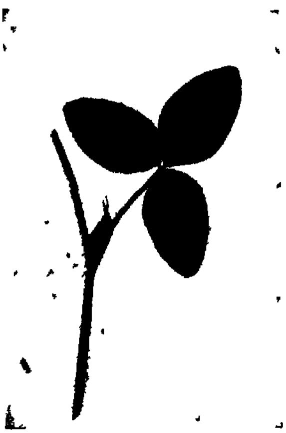


FIG. 9. Palmately compound leaf of red clover.

grasses, have parallel veins. The flowers are small and are of two kinds, one kind in the tassels and the other in the ears. The corn plant is representative of the large annuals.

FIG. 10. Easter lily with large, showy flowers and sessile leaves that have an alternate arrangement on the stem.

Two Great Groups of Flowering Plants.—This brief survey of four well-known plants will serve as an introduction to the two great groups that make up the flowering plants. It was noted that the sunflower and the clover are alike in having leaves with netted veins, while the lily and the corn differ from them in having leaves with parallel veins. If seeds and seedlings are studied it will be seen that the sunflower has two seed

leaves or *cotyledons* while the corn and the lily have but one cotyledon. Hence, we say that the sunflower and the clover belong to the *Dicotyledons* and the lily and the corn belong to the *Monocotyledons.* These two groups may be distinguished (with few exceptions) by three characters: (1) the number of cotyledons in the seed, (2) the veins in the leaves, and (3) the internal structure of the stems, described in Chapter

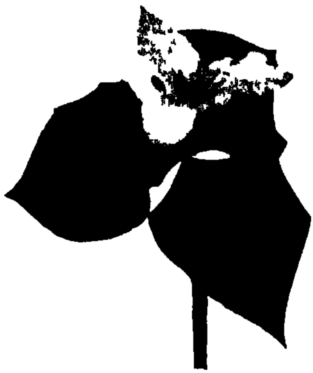


FIG. 11. Upper portion of *Trillium* plant with whorled arrangement of leaves on the stem.

VII. The Dicotyledons constitute the larger group in number of species, but thousands are found in each.

Lilac.—The lilac is representative of the *woody shrubs.* Instead of forming a single trunk its stem branches close to the ground. Each node bears two leaves that are *opposite,* in contrast with the *alternate* arrangement on sunflower, clover, and corn, and the whorled arrangement on some lilies. The leaves of most varieties have smooth margins without notches of any kind and are, therefore, *entire.* The white or purple flowers in loose, showy clusters make this shrub a favorite in thousands of dooryards and flower gardens.

Black Walnut.—A magnificent tree of surpassing beauty is the black walnut. Its trunk may grow to be several feet in diameter. Standing alone it has wide-spreading branches, but in a crowded forest the trunk rises straight and smooth to a great height. A noticeable feature is the great *pinnately compound* leaves, sometimes a foot or more in length, with many large leaflets arranged all along the sides of a central stalk or *rachis.* Trees of the black walnut do not form dense forests but are

FIG 12 Young corn plant with parallel-veined leaves typical of monocotyledons

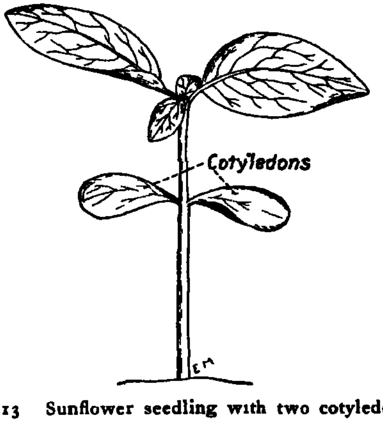


FIG. 13 Sunflower seedling with two cotyledons.

scattered among other trees. The wood makes lumber of dark color and great beauty.

Pine.—The pine tree does not bear true flowers but cones containing seeds. The branches are borne in whorls, a new one usually being added each year. The leaves are needle-shaped and much darker in color

FIG. 14. Twig of lilac with entire leaves that have an opposite arrangement on the stem.

than those of the lilac and the walnut. They persist more than a single season and are therefore called "*evergreen*" in contrast with those of *deciduous* trees, like the walnut, maple, and willow, that are shed every autumn. It must not be supposed, however, that pine leaves never fall off. Their life on the tree is about five years, new ones formed on the younger growth replacing them and leaving the older trunks and limbs bare. The tree has a resinous pitch that oozes out when a wound is made and helps to protect the damaged area.

This survey of a few representative plants should emphasize some of the features to be observed in studying plants and introduce a few of the morphological terms in common use.

Higher versus Lower Plants.—The plant kingdom includes a great assortment of plants, those with which we are most familiar being the seed-producing plants such as those just described. These are grouped into those that produce flowers, the Dicotyledons and the Monocotyle-

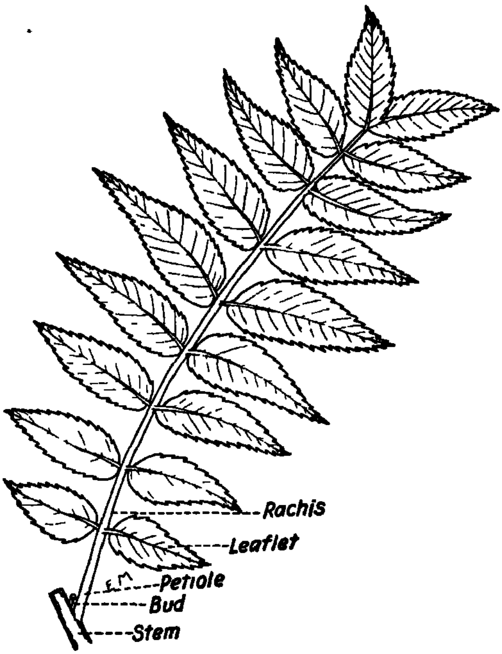


FIG. 15. Pinnately compound leaf of black walnut.

dons, which together make up the *Angiosperms;* and those that produce cones rather than true flowers, the *Gymnosperms,* of which pine, fir, spruce, and hemlock are examples. For convenience we call these the *higher* plants in contrast with simpler forms that do not form flowers or seeds. These we call the *lower* plants. They include ferns, mosses, lichens, the green algae found in ponds and streams, seaweeds, mushrooms, and even the yeast plants and bacteria. When we think of plants we must not exclude these lower forms, some of which have great economic importance.

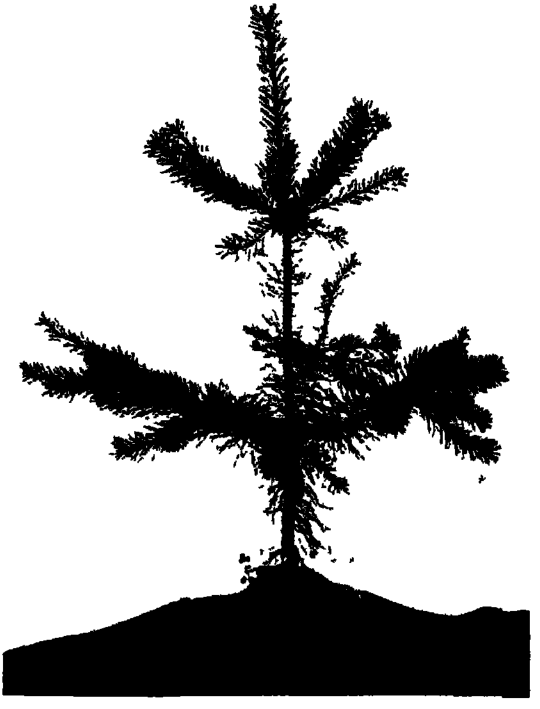


FIG. 16. Small pine tree with "evergreen," needle-shaped leaves and branches in whorls.

REVIEW QUISTIONS

1. Name five industries or *applied* branches of science that are based largely on the use of plants.
2. What value have plants other than monetary?
3. What three parts make up all higher plants?
4. Why not name flowers, fruits, and seeds as additional parts?
5. What name is given to the portions of the stem that bear leaves and branches? To the spaces between them?
6. Name and define three kinds of leaf arrangement based on number of leaves at a node.
7. Give two examples of plants illustrating each of the three kinds of leaf arrangement.

8. Name and define three parts of a typical leaf as seen externally.
9. What term is applied to a leaf that has no petiole?
10. Give a classification of leaves based on the external form of the *blade* and its parts.
11. Give three examples of plants illustrating each kind of blade.
12. What is meant by an inflorescence? Give an example.
13. Distinguish between annuals, biennials, and perennials, and give two examples of each.
14. Into what two great groups are the flowering plants divided? Give two examples of each group.
15. Give two ways of distinguishing between these two groups.
16. Give the distinctions between an herbaceous perennial, a shrub, and a tree.
17. What is the distinction between a deciduous tree and an "evergreen" tree?
18. Which of the following should be classed as "higher" and which as "lower" plants: (1) mushroom, (2) lilac, (3) fern, (4) moss, (5) pine, (6) yeast plant, (7) grass, (8) mold, (9) bacteria, (10) cat-tail.
19. Five examples of flowering plants are briefly described in Chapter I. List these plants in the order of their abundance out-of-doors within a radius of one mile from the institution where you are studying.
20. Each of these six plants is introduced into this chapter to illustrate one or more things about plants. State what each especially illustrates.

CHAPTER II

PLANT BEHAVIOR

Plants are living things—as truly so as are animals. To be living things they must be able to utilize food, grow, and reproduce; and they must be sensitive to changes in their environment, showing appropriate responses to light, gravity, touch, etc. Non-living materials cannot do these things. It is generally agreed that plants have no consciousness and no conscious sensation; nevertheless, their protoplasm is more or less responsive to environmental change. This sensitiveness we call *irritability*. Among the different kinds of plants we find examples of behavior more or less resembling that of animals. Some have considerable power of movement, some climb trees, some catch insects, many of them mate with each other, a few defend themselves from attack, and nearly all can heal simple wounds. There is, however, no attempt to imitate animals; each plant species has evolved these powers independently.

Movement in Plants

An old-time distinction between plants and animals was that animals have the power of locomotion, while plants do not. In the main this distinction will hold, but as a hard-and-fast rule it has been abandoned. Sponges and corals are now known to be animals anchored fast like plants, while some bacteria, diatoms, and other plants of microscopic size swim about freely.

It is well at this time to distinguish between *locomotion* and *movement*. In locomotion the animal or plant changes its location from place to place, while movement may involve only a part of an animal or plant, the rest remaining stationary. Movement of certain parts such as twining stems, tendrils, leaves, and floral organs is very common in the plant kingdom.

Response to Gravity.—We note that the sunflower plant, like most others, stands erect with its roots in the soil and its stem in the air. No matter in what position the seed is planted, the stem, as it emerges,

grows upward while the roots grow downward. Evidently gravity is concerned in these processes.

If we select a straight young seedling growing in a flower pot so that it can be moved about without injury and place it in a horizontal position, the young portion toward the tip will slowly bend upward into the vertical position. This phenomenon is spoken of as *geotropism,* which is one manifestation of irritability. In geotropism there is a definite sequence of events: (1) An outside stimulus, gravity, acts on

FIG. 17. Sunflower seedlings growing in a normal position.

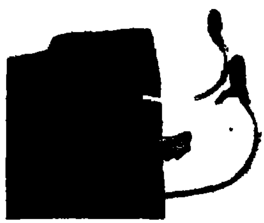


FIG. 18. Sunflower seedlings showing a negative response to the stimulus of gravity when the pot in which they were growing was turned on its side.

all parts of the plant. (2) In the tip of each stem and root and in each petiole there is a *region of perception* of this stimulus, the other parts apparently not being sensitive to gravity. (3) The effect of the stimulus is transmitted through tissues not visibly affected by it to a *region of response* which is an appreciable distance away from the region of perception. Experiment indicates that this transmission is through the diffusion of a growth-promoting substance, or hormone, from one region into the other. Apparently this hormone becomes distributed unevenly, so that one side of the stem or root elongates more rapidly than the other. The time required for this to take place is called the *transmission time* or the *latent period.* (4) There is a visible response which, in this case, is the upward bending of the stem brought about by more rapid elongation in the lower side of the stem than in the upper side. As the bending of the stem is *away from* the earth which attracts it, it is said to be *negatively* geotropic. Roots, on the other hand, tend to

grow *toward* the earth and are *positively* geotropic. Leaves also exhibit geotropism, bending their petioles to bring the blade right side up. Plants thus are shown to have a very important mechanism for maintaining their posture.

While the main stem is negatively geotropic and the tap root is positively geotropic, the same cannot be said of the branches, which tend to grow at right angles to the force of gravity. It is a fact of peculiar interest and of great significance to the plant that if the terminal bud

FIG. 19. Young tomato plants showing a positive response to the stimulus of light reaching them from one side.

of a stem is removed the young branch just below it will change its tendency and grow upward instead of outward, thus continuing the upward growth of the plant.

Response to Light.—If gravity is important in its effect on plants, light is even more so. Light furnishes the chief source of energy, as shown in Chapter VIII, and it also stimulates movement. Many have noted the bending of young seedlings, such as tomato plants, toward a source of light at a window. This phenomenon, *phototropism* or *heliotropism*, is similar to geotropism except for the character of the stimulus. Stems are positively phototropic, as a rule, and most roots are negatively phototropic. The sunflower head turns toward the light through the bending of the stem just below it. The response is not in proportion to the strength of the light stimulus. Plants will bend very definitely toward a weak but continuous light. If a plant is placed for a few minutes where the light comes from one side only, and then is covered

with a dark box, shutting out all the light, it will, at the end of the latent period, bend slightly toward the point once occupied by the light and then straighten up in response to gravity.

Experimentally it is possible to neutralize the stimulus of light or of gravity by slowly revolving the plant on a *clinostat* so that it is constantly turning a different side toward the stimulus. Thus, before the latent period has passed a new tendency to turn in a different direc-

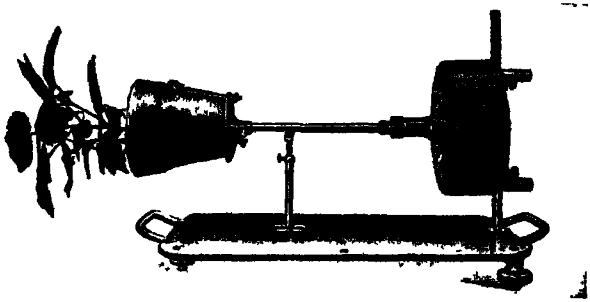


FIG. 20. Clinostat—a machine for slowly revolving a plant on any desired axis, to neutralize the effect of a stimulus that comes from one direction.

tion is set up, and, as a result, the plant does not make a definite response in any direction.

Day and Night Movements.—A phenomenon somewhat different from phototropism is the movement that takes place in plants as light changes to darkness and darkness to light. In the evening, as the light fades, many flowers close until they look like half-opened buds. Well known among these are the crocus, gentian, and water-lily flowers, and the heads of the dandelion. On the other hand, a few flowers open as night comes on, notably the evening primroses, moonflower, and night-blooming catchfly. Likewise, some compound leaves fold up at night-fall, common examples being white clover and wood-sorrel.

It may be questioned whether these so-called "sleep movements" are controlled by light and darkness or whether they would take place at a certain time of the day regardless of the intensity of the light. An ingenious student could think of two or three ways of finding the answer to this question. He could, by the use of artificial light, prevent darkness from striking the plants in the evening, or he could cover them so that at sunrise no light would reach them. More easily, he could carry

potted plants into a dark room and out again at times of day other than morning and evening. Such experiments have shown that some of these movements in plants are responses to light intensity, not to a definite time of day.

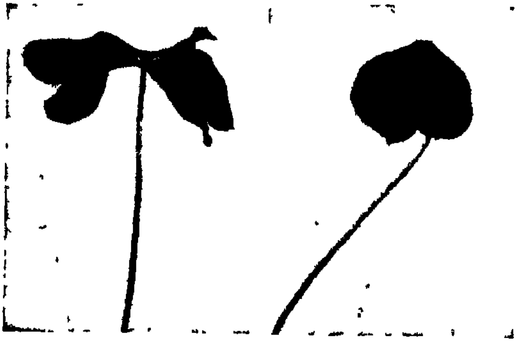


FIG. 21. Leaves of wood-sorrel. A, exposed to strong light; B, placed in darkness, the leaflets folding together by a "sleep movement."

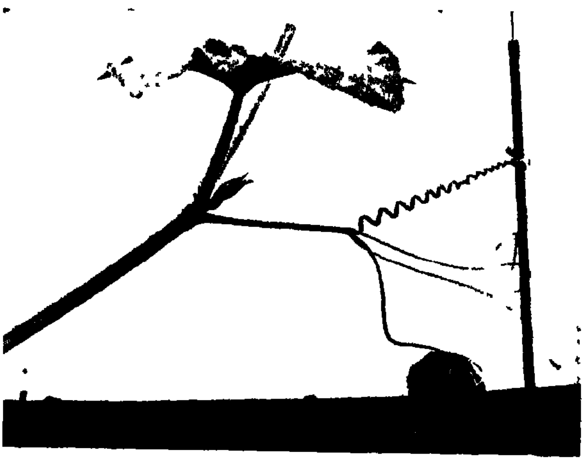


FIG. 22. Tendril of squash attached to a slender rod. Note that a portion of the tendril twines clockwise and a portion counter-clockwise. If the tip of an extended tendril attached itself to a support, and then the plant was drawn close to the support by a further twining of the tendril in *one direction only, there would be a tendency to twist the tendril off.*

Another stimulus, however, is often responsible for morning and evening movements of flowers and leaves. This is temperature; and as the temperature falls when darkness approaches and rises with the

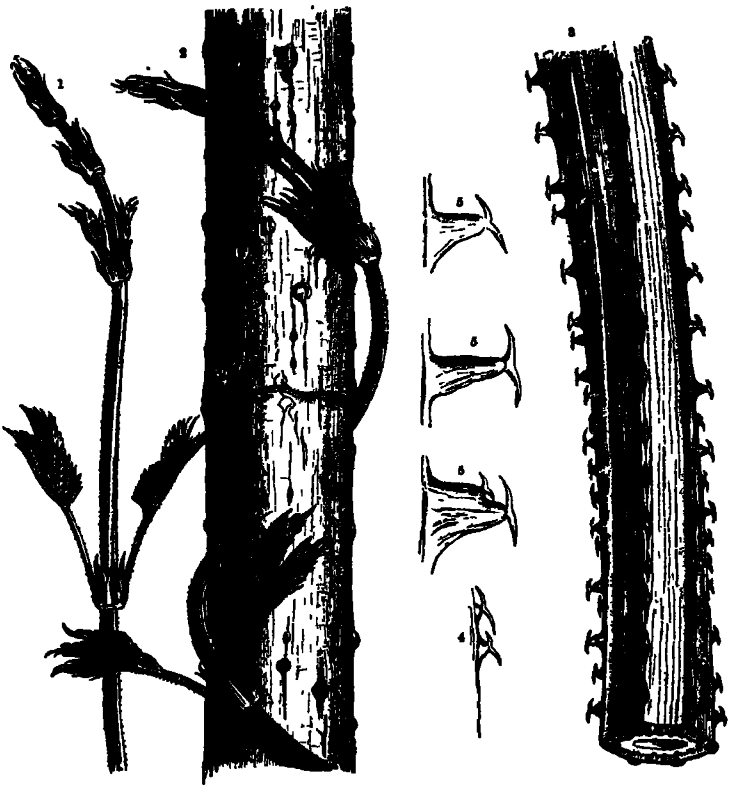


FIG. 23. Hop stem twining about a support. Figures 3, 4, and 5 show roughenings on the stem that prevent slipping. (From Kerner's *Natural History of Plants*, Blackie & Son.)

dawn, careful experiments are required to determine whether light intensity or temperature is responsible for the change in a given plant.

Response to Touch.—When tendrils of climbing plants such as grapes, woodbine, and peas come in contact with a wire or other support, they twine about it. Without such contact they remain relatively

straight, but may eventually coil up by themselves. The coiling of a tendril or twining of a stem about a supporting object illustrates *thigmotropism*. The most noticeable response is a bending at the point of contact, but in the case of a tendril, the close observer will discover another. About half-way between the place of attachment and the base

FIG. 24. Sensitive-plant. One leaf is responding to the stimulus of touch. (From Pfeffer's *Physiology of Plants*, Clarendon Press, Oxford.)

of the tendril another bend takes place. Above this bend the tendril coils in one direction and below it in the opposite direction. The result is that the stem is drawn closer to the support, and a better opportunity is given for other tendrils to catch hold. A little study will show the mechanical necessity for the double spiral rather than a single one below the point of attachment. If, after the tip has become attached, the tendril should attempt to wind around in one direction only, there would be a tendency to twist it off.

A similar, but not identical, illustration of thigmotropism is the twining of the entire stem of hops and morning glories about a pole. If there is no support the end of the plant waves round and round for a

time without much bending, but if a vertical pole is set within its reach it twines closely about it. In the case of the hop plant the stem is very rough and this helps to keep it from slipping down the support.

These twining movements are rather slow, but there are others more rapid. The sensitive-plant has doubly compound leaves with the power of movement. If any part of a leaflet is touched or slightly burned

FIG. 25. Venus fly-trap. The leaves are highly specialized and capable of catching insects. (From Kerner's *Natural History of Plants*, Blackie & Son.)

with a tiny flame a quick response follows. If the stimulus is very slight the stimulated leaflet and its mate fold together upward. If it is somewhat stronger all the leaflets in that part of the leaf fold together in succession. If it is still stronger all the leaflets on that entire leaf fold together, and the petiole bends sharply downward at a basal swelling, the *pulvinus*, which acts as a joint or hinge. After a time the leaf slowly resumes its original position. These sensitive-plants are fascinating for study, but if one stimulates the leaves again and again as soon as they recover, another fact is learned. Repeated stimuli fail to bring a response. In a breeze, when the leaves are being constantly shaken and more or less rubbed together, they will give almost no response to touch.

Even quicker response is given by the Venus fly-trap. In this plant the two halves of the terminal portion of the leaf are hinged on the midrib like jaws. Each half bears three stiff, sensitive hairs. If one of these is touched, the leaf is made more sensitive, so that a second touch to the same hair causes the jaws immediately to shut together—not with a snap but quickly enough to catch any but the most active insects.

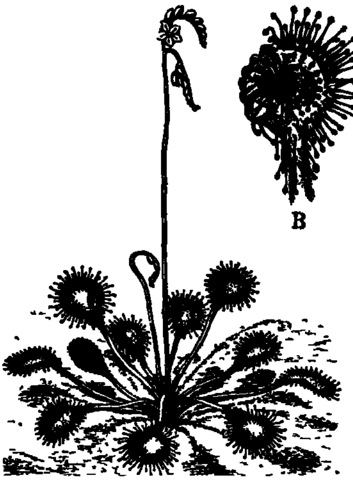


FIG. 26. Sundew. A, entire plant with specialized leaves that catch insects; B, a single leaf with tentacles folding down to a point that has been touched (From Brown's *Textbook of General Botany*, Ginn & Co.)

In another insect catcher, the common sundew, each of the basal leaves bears a disc about a half-inch in diameter. This disc is studded with knobbed, sticky tentacles. If a small insect comes in contact with one of these it sticks fast, and all the other tentacles slowly fold down on top of it and digest it for food. No matter what part of the disc is stimulated, all the tentacles bend to that spot with perfect accuracy.

Nutation.—The movements just described are in response to *external* stimuli. There are other movements inherent in the plant itself and not dependent on an external stimulus. One of the best known of these is nutation. The stems of most young plants seem to the casual observer to grow straight up without any movement except that produced by the wind or other outside force. Close observation, however, shows that the tip moves slowly round and round. The combined effect of this nutation and upward growth is to give the tip of the stem a spiral motion. It is often assumed that a plant benefits by anything that it does regularly and normally, but the nature of the benefit in this case is not obvious.

The Mechanism of Movement in Plants

By this we do not mean the stimulus that induces a plant to move its parts but the means by which the movement is accomplished.

Higher animals move their parts by the contraction of muscles, using the bones as levers. Plants, having no muscles, must bring about movement by other means. The commonest mechanisms of movement in plants are two—uneven growth and uneven shrinkage through loss of water.

In geotropic and phototropic responses and in the twining of stems and tendrils, one side of the stem grows faster than the other side, thus pushing the stem into a bent position. When the sensitive-plant is touched it loses water from the pulvinus. This brings about a loss of turgor and an uneven shrinkage which pulls the leaf or leaflet into the new position. When seed pods and capsules dry, different parts lose moisture and shrink unevenly, bringing about a strain which causes them to snap open and release the seeds.

In the study of irritability plant physiologists have used great ingenuity in devising experiments to solve significant problems. Among these problems are: (1) the location of the region in the plant which is sensitive to the stimulus, (2) the method by which the impulse is communicated to the region of response through tissues that are neither sensitive to the stimulus nor capable of responding to it, (3) the minimum strength of the stimulus necessary to bring about a response, (4) the mechanism by means of which the plant moves its parts, (5) the nature of fatigue when a plant refuses to respond longer to repetition of the same stimulus, and (6) the entire phenomenon of the locomotion of free-swimming microorganisms.

Protective Mechanisms

Interesting devices of various kinds have been evolved which serve to protect plants from injury, since, being anchored to the ground, they are unable to move out of the path of danger. The outer layer is generally tougher than the delicate tissues inside, and this condition approaches perfection in the hard, corky bark of trees. Thorns, like those of the rose and hawthorn, and stinging hairs, as found on the nettle, help to ward off animals. Ill-tasting and poisonous chemical products serve somewhat the same purpose. Thick, hairy coverings, waterproof coatings, and other devices described later help to reduce excessive evaporation of water. Greater ability to withstand the low temperatures of winter is obtained by the shedding of leaves and by a dormant condition of stems and roots, bulbs and tubers, some of these being buried in the soil where changes in temperature and in moisture

content are less extreme or less sudden than in the air, and through the agency of dry dormant seeds.

Teleology or Teleological Reasoning

There is a very natural error into which many people fall. They assign a purpose, almost a conscious purpose, to many things that plants do. For example, they say that a plant bends upward to get its stem erect, or bends toward the light to get more of it, or makes thorns to protect itself against animals, or produces an excessive number of seeds because some are likely to be destroyed, or produces large, white, fragrant flowers to attract insects. Actually these things usually benefit the plant in the ways indicated, but they take place regardless of whether or not the plant will have need for them. The plant is so constituted that it has to do them regardless of their value to it in any given circumstance. Thus a rose would produce thorns even if there were no animals. An apple would produce showy flowers even if there were no insects, and a mustard plant would produce many seeds even though all of them were sure to grow into plants.

Plants cannot anticipate their needs but develop in accordance with certain laws of inheritance, influenced more or less by their present, but not by their future, environment. For example, in the course of their evolutionary development from more primitive ancestors, variation resulted in the development of certain structures by some plant lines but not by others. If these structures helped the line to fit its environment and survive better than it could have done without them, they became established as *adaptive* structures that aid in adjusting the plants to their environment. The production by many plants of thorns, great numbers of seeds, materials that give fragrance to flowers, and many other structures and materials probably originated in this way and is perpetuated from generation to generation with little regard to present or future need.

This kind of reasoning is spoken of as *teleological*. It indicates a faulty viewpoint and should be avoided. It can hardly be expected that the habit of describing the behavior of plants in teleological terms can be changed among people in general, but students of botany should learn to say that organs are formed and do help the plant rather than that the plant produces these organs in order to accomplish certain things.

Effects of Anesthetics

The effects of anesthetics—ether, chloroform, etc—in deadening the sense of pain in animals are well known How about their effects on plants, which have no sense of pain? This subject has been studied extensively in recent years It has been found that the power of the sensitive-plant to respond to touch and of other plants to respond to the stimuli of light, gravity, etc, is inhibited by ether, chloroform, and some other chemicals that have been classed as anesthetics through their action upon man Thus the effect of these substances on physiological activities seems to be closely similar in plants and in animals

Some of these chemicals have a very different effect that is not to be confused with anesthesis Dormant buds, bulbs, tubers, etc, generally pass, in late summer or autumn into a dormant condition that lasts for weeks or months However, under the influence of ether or chloroform gas in strong dosage the rest period is shortened, and, under suitable growing conditions, activity is renewed at once Similarly, practical use is now made of ethylene in hastening the ripening of citrus fruits and bananas

In this chapter only a few types of plant behavior are illustrated Methods of obtaining food and water of attracting insects of distributing their seeds, etc, are discussed in later chapters of this book

Review Questions

1 Name all the properties that distinguish living from non-living things
2 Just what is meant by irritability?
3 Name five different stimuli to which plants react
4 What is the commonest visible reaction of plants to external stimuli?
5 Distinguish between locomotion and movement
6 Describe two kinds of mechanism by which plants move their parts and give two examples of each
7 What is meant by a "tropism"?
8 In discussing "tropisms," what do we mean by "positive" and "negative"?
9 What parts of a stem are reached by the stimulus of geotropism?
10 What part of the stem in most plants is sensitive to the stimulus of geotropism?
11 What part of the stem responds to this stimulus?
12. In what form is the stimulus transmitted from the sensitive region to the region of response?
13 What is meant by the transmission time or latent period?

14. How does the geotropism of the branches of the stem and the branches of the roots differ from that of the main stem and main root?
15. Of what use is geotropism to a plant?
16. Of what use is phototropism to a plant?
17. What are the successive steps that take place in phototropism?
18. Give two examples of thigmotropism in plants.
19. Describe the coiling of an attached tendril and explain the necessity for this style of coiling.
20. What two stimuli are responsible for the closing of flowers and the folding of leaves in the evening?
21. In a given case, how could you determine which of these is responsible?
22. Name two effects of ether on plants.
23. State what is meant by teleology or teleological reasoning, and give two examples of your own devising.
24. What could you do to a plant, without seriously injuring it, to make it unable to respond to stimuli?
25. The statement has been made that the stems of plants bend toward the sun because it is warmer on that side. How could you determine experimentally whether or not this conclusion is justified?

Part Two

PLANTS AND THEIR SURROUNDINGS

CHAPTER III

ROOTS AND THE EARTH IN WHICH THEY LIVE

It is characteristic of most land plants that the basal portion is attached to the earth or some other solid object from which it derives a part of its nourishment. The lower plants that live in water—the seaweeds, etc.—are likewise attached to the bottom in most cases, but the purpose served is chiefly anchorage rather than food absorption.

Soil, the Environment of Roots

Ages ago plants flourished in the sea, but none grew on land. These plants were simple in structure, for higher forms had not yet evolved. The land at first was rocky and uninhabitable, but as a result of weathering, soil of a mineral nature was formed. By wave action plant and animal bodies were thrown upon the shores and through decay became incorporated in the soil. Presumably it was then that terrestrial plants arose through evolution from the lower forms. From that time to the present they have played a major part in the formation of our fertile soils.

The soils of today are variable, containing, in different proportions, (1) disintegrated and decomposed rocks of various kinds, (2) organic matter from plants and animals, (3) air spaces, and (4) water holding chemicals in solution. If the organic material is so far decomposed that its original character is no longer recognizable, it is called ***humus***. This term should not be applied to leaves, roots, or other organic matter in early stages of decomposition.

The great value of humus to the soil is universally recognized. It adds to the mellowness of the soil, it increases its water-holding capacity, and it affords a reserve supply of food material for plants. It is found abundantly where plenty of vegetation is regularly added to the soil, either naturally or through the agency of man, and where the moisture supply is plentiful.

The water content of soils is of great significance. In different areas every variation can be found from that of the swamps of Florida

to that of the Sahara desert. Water in soils is recognized in three forms. (1) *Gravitational* water is that which flows freely downward between the soil particles during and following rains or melting snow, or as a result of irrigation. Ultimately it reaches a depth where its further passage is blocked and water continuously fills the spaces, saturating the soil and excluding the air from it. This level is called the

FIG. 27. Root-hairs penetrating the soil Note the tiny rock particles, the bits of humus, the films of water, and the air spaces

water-table, and it may rise and fall or it may remain fairly constant. (2) *Capillary* water is that which adheres as films to the soil particles. Its source is largely the gravitational water, which wets the particles as it passes through. (3) *Hygroscopic* water is that which still remains in a soil after it has been air-dried, although it can be driven off, for the most part, by heating above the boiling point. It is mostly contained within the organic matter or other colloidal material, which is more or less swelled by its presence. From which of these does the living plant obtain its supply? The gravitational water passes so quickly that it does not furnish a continuous source. Usually the water-table is so low that few, if any, of the roots are able to reach it. The hygroscopic water is held so tenaciously by the soil particles that the roots are unable to extract it to any great extent. The capillary water,

however, in most soils is continuously available and is readily taken up by the roots.

Soils differ much in their water-holding capacity, i.e., in the amount of water they can absorb and retain from the gravitational water passing through. As the water thus retained is a combination of both hygroscopic and capillary water, it is obvious that to have a high water-holding capacity a soil must be rich in organic matter, with finely divided, well-separated, mineral particles offering a large total surface for films of moisture. In a sandy soil the particles are relatively large and the water-holding capacity is correspondingly low. The particles in a clay soil lie so close together that water passes through it with difficulty and it retains water tenaciously. A loamy soil is a mixture of sand and clay and has a high water-holding capacity, especially if it is rich in humus and is kept loose by cultivation.

In Chapter VII the method by which plants obtain water from the soil will be explained in detail.

Plant Adaptations to Different Amounts of Soil Water.—During the course of time seeds of many kinds have become widely distributed over the earth. The plants growing from them have encountered a wide range of conditions, including those offered by soils of different degrees of moisture. More important still, geologic changes have converted swamps into deserts and deserts into swamps from which plants have found difficulty in migrating. In the changed environment many species failed to survive the unfavorable conditions brought about by too much or too little water. Other species, through successive generations, adapted themselves to the new environment by undergoing structural or physiological changes. What then are the adaptations that fit plants for much or little soil moisture, the latter usually being accompanied by low humidity of the air? Aquatic plants generally have a scarcity of root-hairs, often weak stems, as those of water-lilies, and sometimes air-bladders or floats, as illustrated by the water-hyacinth. Usually their leaves are on or above the surface of the water and relatively large. If submerged, however, they may be mere skeletons composed mostly of veins. Most aquatic plants differ from other kinds in having large air passages in their submerged parts, which carry oxygen from the leaves to the roots, where it is used in respiration, and carry the carbon dioxide formed in this process back to the leaves, where it is either used or given off into the air, thus preventing the formation of carbonic acid in the soil and consequent injury to the roots. These plants have also undergone certain physiological changes which make

them more adaptable to an aquatic mode of life but which are not fully understood. Such plants are called *hydrophytes.*

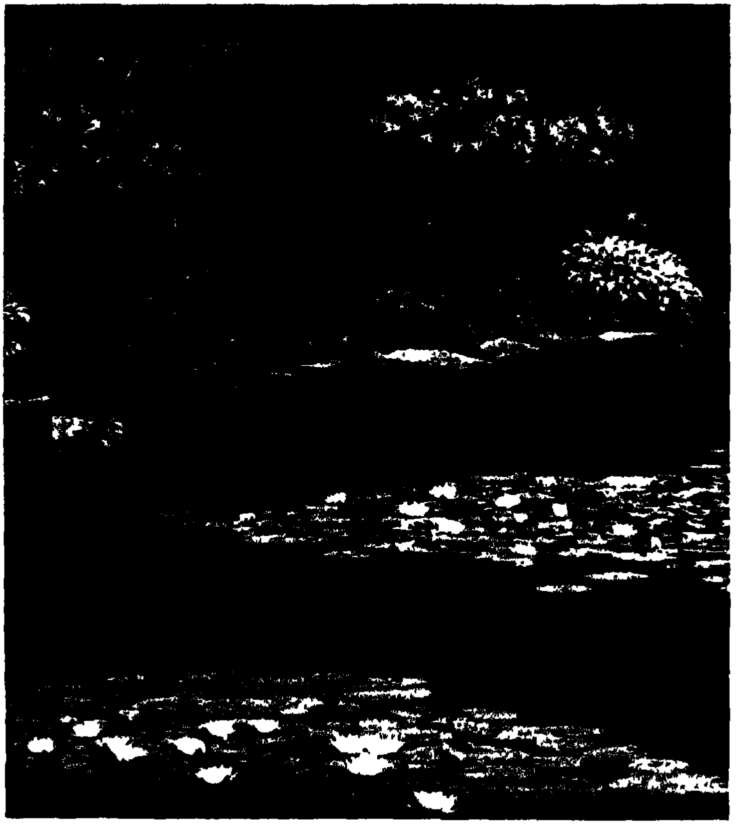


FIG. 28. White water-lilies. Typical hydrophytes. (From Dixon's *The Human Side of Plants,* Frederick A. Stokes Co.)

Plants adapted to growth in desert regions are *xerophytes.* They have either long, deeply penetrating roots or an abundance of very superficial ones that take the maximum advantage of occasional light rains. Some species have both. In many species the stems are short and the leaves narrow and relatively thick, permitting a minimum of evaporation. Others, however, have thin, broad leaves together with an

extensive root system for absorption of water. Often there are special devices such as hairs or folds to reduce evaporation, and the air pores entering the leaf are few in number, small, or so shaped as to prevent loss of water. Some xerophytes contain materials such as gums and mucilage that hold water most tenaciously. A few have structural modifications that are truly remarkable, some of which are described in Chapter VII.

The great majority of plants, like the sunflower and most of our crop plants, are *mesophytes* that thrive in soils of moderate water content and have no special structures like those of hydrophytes and xerophytes.

The Acidity of the Soil.—Most soils are approximately neutral in reaction, but some are somewhat acid and others somewhat basic. In the eastern United States, where the rainfall is relatively heavy and soil aeration is often poor, the tendency is toward acid soils. The acids present may be either organic or mineral in nature. Carbonic, acetic, lactic, nitric, hydrochloric, and sulfuric acids are common. Their presence is due to a number of causes—their production by the action of certain bacteria and by the decomposition of salts, and the lack of basic ingredients in the soil to neutralize the acids thus formed. Acid soils are unfavorable to the development of most plants, either through direct injury to their roots or by indirect action through the suppression of bacterial activities or the bringing about of an unfavorable physical condition in the soil.

In the arid regions of the far western states and on the shores of bodies of salt water there is often an accumulation of soluble mineral salts commonly termed alkali. Such alkali salts include carbonates, chlorides, nitrates, and sulfates, of which only potassium and sodium carbonates are basic in reaction. Under some conditions ammonium hydroxide may be present also. These accumulations of salts are, for the most part, due to the decomposition of rocks where precipitation is insufficient to leach away the resulting products. Most of them are good food materials for plants when not present in too large quantity.

When present in too high concentration these alkali salts delay seed germination, interfere with the absorption of water, thus causing wilting, and even bring about a withdrawal of water from the roots. They make the soil relatively impervious to water and in extreme cases cause direct damage to the roots.

A few plants are adapted to life in soil that contains an unusually high percentage of alkali salts. These are classed as *halophytes* and are popularly termed "alkali plants."

Importance of Air in the Soil.—It has long been known that most mesophytic plants do not thrive in water-logged soil. Air is necessary for the health of the roots. If the soil is saturated with water most of the air is excluded from it. Brief periods of saturation, as during a heavy rain, seem to be well tolerated by the plant, but if long continued, as by a rise in the water-table, an unhealthy condition develops in both roots and leaves. Under these conditions root-hairs die and are not

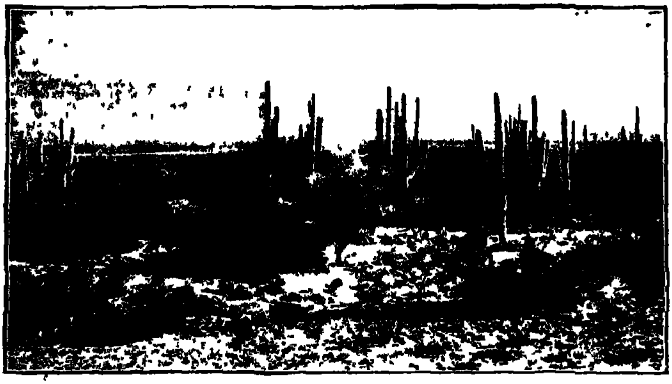


FIG. 29. An Arizona desert with giant cacti and other xerophytes. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc Original by Dr. Forest Shreve, Laboratory of Plant Physiology, Tucson, Arizona.)

replaced by others. Small rootlets may also die, and quite regularly the formation of new branch roots is inhibited. The leaves may wilt even though the soil is filled with water, and they soon turn yellow and drop off.

These conditions have been ascribed to a shortage of oxygen for respiration and to an accumulation of carbon dioxide in the water close to the roots, making a weak solution of carbonic acid. It may be noted that hydrophytic plants are not adversely affected by lack of air about the roots, but they generally have internal air spaces that supply the roots from above.

Adaptability of Plants to Different Soil Conditions.—Plants vary in their preference for different types of soil. A few are adapted to a sandy soil with little organic matter, but the majority thrive best where there is an abundance of humus. This is relatively insoluble and serves as a storehouse of food materials which gradually undergo chemi-

cal change and are thus brought into solution and absorbed by the plants. A few species prefer slightly acid soil, and a few prefer an excess of alkali, but, for most species, a soil that is practically neutral in reaction is most favorable. Adaptability to water content of soils has already been mentioned.

The welfare and behavior of plants and, indeed, their very existence are largely determined by their environment—the soil and the air, temperature, light, food supply, etc. *Ecology* is an important branch of botanical science that treats of the relation of plants to their environment. Chapter XXVII, page 409, and XXVIII, page 416, consider certain aspects of Ecology. Since it deals with the adaptability of plants to the places in which we wish to grow them, the effects of unfavorable conditions, of crowding, over-grazing, and over-cropping, this subject has extensive applications in forestry, soil conservation, and other branches of agriculture.

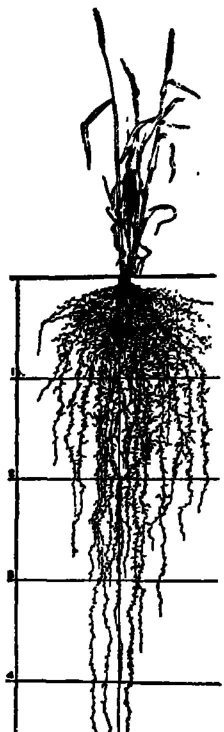


FIG. 30. Root system of wheat plant at blossoming time. Figures indicate depths in feet. (From Weaver's *Root Development of Field Crops*, McGraw-Hill Book Company, Inc.)

ROOTS AND THEIR BEHAVIOR

Largely by means of roots, plants take advantage of the terrestrial environment, and this has made possible the advance of flowering plants over seaweeds. The firm anchorage, enabling the stems and leaves to rise into the air and light, the necessary water, and the mineral portion of the food—all these are supplied by the roots. The adaptations of roots to make these necessary contributions to the life of plants are of more than passing interest.

Roots as Anchors.—To anchor plants to the best advantage, the root system must be long, strong, and extensively branched. The strain brought about by a heavy wind on a great tree is enormous.

Hidden as it is by the earth, few people appreciate the extent of the root system of a plant. Often the nortion below ground is as great as

that above. In many desert plants it is much longer. Even the mesophytic wheat plant sends its roots as much as five feet into the soil, while alfalfa roots often penetrate to a depth of twenty feet and sometimes to twice that depth. The principal feeding area, however, is at a higher level. As a rule, a root is as strong for its size as a stem, and sometimes it is even stronger, especially in herbaceous perennials. The root system is so intricately branched that it is impossible to remove it all from the earth. Even though the ground is very soft and the digging and washing are done most carefully, many of the smaller branches are broken off.

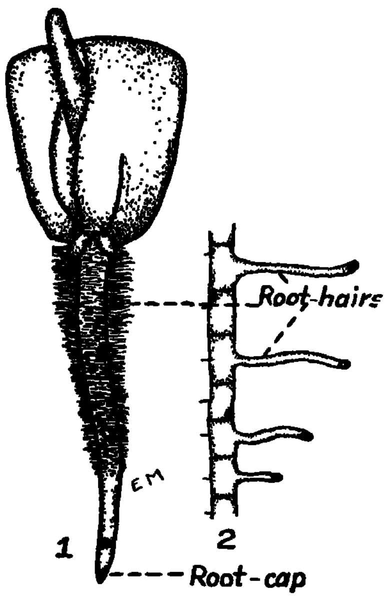


FIG. 31. 1, germinating corn seed, showing tap-root with root-hairs just back of the tip and root-cap at the end. 2, root-hairs more highly magnified.

Enough may be removed, however, to show that roots differ considerably from stems in their method of branching. No nodes are to be found on roots, and the branching appears more irregular. Undoubtedly there is a determining factor that causes each branch root to be sent forth from a definite point, but its nature is obscure.

Roots as Absorbing Organs.—Without water most plants quickly die. Without mineral food materials they could not continue to live and grow for a great length of time. By what devices, then, can absorption from a soil, often too dry for the welfare of the plant, be most effectively accomplished? The student who understands the nature of absorption will at once realize that an effective mechanism for this purpose must have a large absorptive area and be easily permeable. Such a condition is found to perfection in a well-developed root system. The bark on the old roots is thick and hard and absorbs little water, but even on the oldest trees there are myriads of young branch roots that absorb a little water directly through the epidermis and countless *root-hairs,* which are the special organs of

absorption. These hairs are borne on a region just back of the root tip and penetrate the spaces between the soil particles where capillary water is found. They are thin-walled, delicate extensions of epidermal cells into the soil from which they absorb both water and mineral matter. (See Fig. 27, page 40). If through accident, as when transplanting is done, the root-hairs are stripped off or killed, the general surface of the root will absorb a little water, enough usually to keep the plant alive

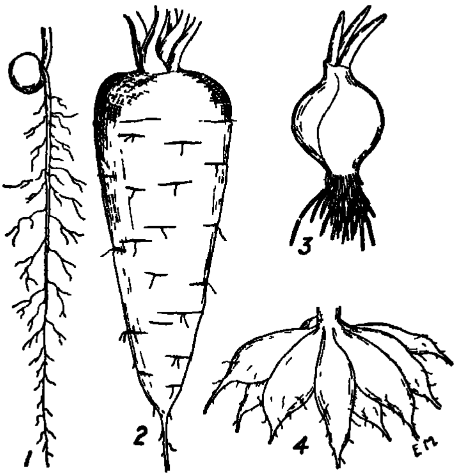


FIG. 32. Different kinds of roots. 1, fibrous tap-root of pea; 2, fleshy tap-root of carrot; 3, fibrous fascicled roots of onion; 4, fleshy fascicled roots of dahlia.

and start new roots that send out root-hairs of their own and thus re-establish normal absorption.

As long as plants live they grow, and the tiny rootlets are pushed farther into the soil. This may be very hard, and the delicate tips would be seriously injured but for a protective *root-cap,* which constantly wears away as the root progresses and is as constantly being renewed from within. As the root grows in length new root-hairs appear toward the tip, and the old ones farther back wither away. It should be understood that growth takes place at the tip or very close to it and that the region bearing root-hairs is never pushed through the soil, which would, of course, strip them off.

Kinds of Roots.—Most plants, like the sunflower, send down one main *tap-root* which bears many lateral roots. Some, however, as the

onion and most grasses, produce, instead, a considerable number of *fascicled* roots, all about the same size. Extensive storage of food is accomplished by *fleshy* roots, which may be either tap-roots, as those of the radish, or fascicled as those of the dahlia. Some of the palms, corn, tomato, and a few other plants tend to bend over from insufficient anchorage, and this weakness is remedied by *prop roots* that start from the lower parts of the stem and grow down into the soil. Banyan trees make an astonishing development of prop roots, which start in great numbers from branches several feet above the ground and grow downward into the soil, making a small forest of supports.

While most roots arise as branches of other roots, some originate in stems or leaves, and these are called *adventitious roots.* Adventitious roots from stems start from the nodes or, less commonly, from the internodes (Fig. 88). They make possible the propagation by cuttings of many plants, including willow, geranium, and wandering Jew. Leaves give origin to roots in only a few plants, of which the begonia is an example. Adventitious roots may start from stems above ground and never reach the soil. In this case they are called *aerial* roots. Such roots occur on some tropical orchids, as well as on the English ivy where they aid the plant in clinging to walls.

Review Questions

1. What kinds of plants should be contrasted with terrestrial plants?
2. Give two advantages to plants of being anchored to the ground.
3. What has been the origin of most of our soils?
4. Describe the structure of a common fertile soil.
5. What is the distinction between organic matter and humus?
6. What name is applied to water in each of the following states in a soil: (1) flowing down through it? (2) clinging as films to the solid particles? (3) absorbed by the organic matter? (4) standing in the soil spaces?
7. Which one furnishes the most water to the roots of plants?
8. What three factors determine the water-holding capacity of a soil?
9. What causes the injury to ordinary plants in a water-logged soil?
10. Why are not hydrophytic plants injured by a water-logged soil?
11. As the climate and soil moisture in different regions of the earth changed, what determined whether or not the kinds of plants that were growing there survived?
12. What term is applied to plants adapted for growth in desert regions?
13. What term is applied to plants adapted for growth in very wet places?
14. Name the morphological characteristics of a hydrophyte.
15. Name the morphological characteristics of a xerophyte.

16. What term is applied to plants adapted for growth in soils containing excessive amounts of soluble salts?
17. Give an approximate idea of the depth to which the roots of some of our mesophytic plants penetrate.
18. In what two ways are the root-hairs especially adapted for absorption?
19. How does a root-hair differ from a branch root: (1) as to structure? (2) as to length of life?
20. Explain how the delicate tip of a root is protected while pushing through a hard soil.
21. Name and define five kinds of roots.
22. Name two plants that have prop roots.
23. Give three functions of roots.
24. Explain why a fine sand can hold more water per cubic foot than coarse sand.
25. Why is it better for the roots of a plant to elongate by growth at the tip only rather than to elongate throughout their entire length?

CHAPTER IV

AIR AS A PART OF THE ENVIRONMENT

Ancestral plants, submerged in the ocean, had little contact with the air. When part of them began a terrestrial life they faced new problems, some of which were most difficult of solution. They were no longer buoyed up by water. To obtain the full benefits of the air and sunlight they must develop strong stems and stand erect, supported by their roots. When erect they were buffeted by the winds. Most serious of all, they were exposed to danger from evaporation of moisture and must raise water through their stems to their leaves. It might seem, then, that water is a better habitat for plants than air. Observation shows, however, that such is not the case, for land plants have made much more rapid evolutionary progress than submerged plants. Evidently the advantages of stronger light and a good supply of food materials in the air more than offset the difficulties encountered by living on land.

Advantages of a Terrestrial Environment

For many centuries after plants appeared in the sea the evolution toward higher plants appears to have been very slow, resulting in only relatively simple seaweeds that were not differentiated into true roots, stems, and leaves and bore neither flowers nor fruits. Even today none of the very highest plants, and few seed-plants of any kind, grow submerged entirely in water.

When plants became established on the land, evolutionary progress was more rapid, and there appeared mosses, ferns, and seed-plants—the latter now being the predominant vegetation of the earth.

In some respects a terrestrial environment is more favorable for plants. From the water they can obtain both oxygen and carbon dioxide, which are dissolved in it, and some mineral food materials in solution; but fertile soils furnish even more mineral matter to land plants. The greatest advantage of all lies in the increased amount of light for energy which becomes available to them, for while the light of the sun pene-

trates water to some extent, its intensity diminishes rapidly with the depth of the water.

With respect to temperature changes, the submerged plants have an advantage, for such changes are much more sudden and cover a wider range in air than in water.

Effects of Light

Without light there could be no life. Even though a few animals and lower plants live in dark places, it is nevertheless true that directly or indirectly the light of the sun supplies energy for practically all living things. The importance of light in food manufacture by green plants will be discussed in detail later.

In addition to the movements of plants in response to the light stimulus there are some other light effects worth considering. The color of most plants is largely determined by the presence of light. In a dark room, or when covered by an opaque object for a few days, green plants turn yellow or nearly white. When returned to a strong light they are liable to sun-scald, but if this does not occur they regain their color in about the same length of time it took them to lose it or even more quickly.

Effect on Growth.—Why are trees in a thick forest or plants growing in the shade taller in proportion to their diameter than others standing alone in strong sunlight? Light appears to be a determining factor. Contrary to general belief, plants actually elongate more rapidly at night than in the daytime, provided there is an abundance of food. Sprouts from potato tubers in a nearly dark cellar may grow to a length of four or five feet, while those from other tubers planted in the ground and growing up into the light for the same length of time will be no more than a foot high but stockier in build and stronger. In general, the mechanical or supporting tissue of stems is poorly developed if plants are grown in darkness. Furthermore, the leaves on plants grown in darkness are very small, although if grown in shade they may be a little broader than if grown in direct sunlight.

Ways of Increasing Light Absorption.—It is well known that light intensity varies widely in different regions and at different times. It is not so easily measured as temperature, and no instrument for measuring it is in common household use, although such instruments, based on the photoelectric cell, have been devised for technical work. The intense, direct sunshine is stronger than is most favorable for the ma-

jority of plants, but the diffused light of shade is far too weak. Even in regions of greatest light intensity, fewer than half the hours of the daily twenty-four yield a sufficient amount, and yet plants could use light continuously if supplied with it, as has been shown by experiments with artificial lighting. It is evident, therefore, that structural modifications that enable green plants to receive more light must be advantageous,

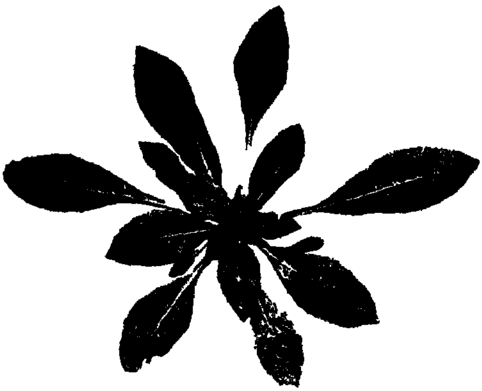


FIG. 33. Young plant of evening primrose with leaves arranged in a rosette, in which position they receive the maximum amount of light. Viewed from above.

while devices for enabling them to avoid too much light are less frequently needed.

Without a conscious purpose to benefit the individual or its offspring, plants have acquired several structural adaptions for increased light absorption. Of these, flatness of the leaves, by means of which a large surface is exposed to the light, is the most important. However, leaves have a tendency to shade each other, and this tendency is partly overcome in several ways. (1) Leaves are borne mostly at the tips of branches, the main limbs toward the trunk where they would be shaded being devoid of them. (2) The tops of many trees are conical in shape, thus exposing most of the leaves to the direct sunlight for a maximum period of the day. (3) Many herbaceous plants with very short stems have their leaves arranged in rosettes, the lower ones largest and the younger ones smaller and covering them but slightly. (4) Petioles, by their varying

length and by their bending movements, place the blades in positions where light is most intense. (5) As a result of phototropism, stems that are partly shaded push into open spaces where the light is greater.

Methods for enabling plants to avoid the full intensity of the light are few and simple. (1) The leaves may be narrow and relatively thick. (2) They may be set vertically so that the noonday sun will strike the surface obliquely. (3) Action of the petioles may turn the blades edgewise to the source of light when it becomes too intense.

Effect on Seed Germination.—Seed germination is generally favored by darkness, although in a few species the reverse is true. As seeds are usually in a dark soil when they germinate, this tendency is conducive to prompt development of new plants.

Effects of Temperature

Life can exist only within a limited range of temperature. This range is narrow compared with the extremes we know to exist. We speculate on the possibilities of life as we know it on other planets, and the answer is, in some cases, obviously negative because of the unfavorable temperature that exists there. What then is the range of temperature for life? Why is it so narrow? And what devices, if any, do plants have for extending their temperature range or for tiding over short periods of unfavorable temperature?

In the first place it should be clearly understood that extremes of temperature affect plants in two ways. (1) They may kill the plants outright, or (2) they may inhibit their activities. Flax has a temperature range for seed germination from 35° F. to 82° F., but the pumpkin, a subtropical plant, has a corresponding temperature range from 56° F. to 115° F. Certain lower plants—a few species of bacteria and blue-green algae—thrive in hot springs at temperatures up to 180° F., while other bacteria multiply in soils at the freezing point, and some seaweeds in arctic regions develop freely in ice-water below 32° F. Thus it is seen that different species have different temperature requirements for normal development. In a broad way, flowering plants cannot carry on their activities below the freezing point of water (32° F.) or above the hottest out-of-door temperature in the sun (about 150° F.). Probably no one plant or species has a temperature range for its activities anywhere near so great as those just indicated, for tropical plants cannot develop at a temperature approaching the freezing point, and arctic and alpine plants

would cease to function considerably below the maximum for tropical plants.

Some plants in a dormant state, in which they contain little water, survive great extremes of temperature. Thus seeds have been found to survive when submitted for a short time to the temperature of liquid air (about —360° F.), and bacterial spores may resist boiling for an hour or more.

When succulent plants are frozen, water is withdrawn from the protoplasm and deposited as ice crystals in the air spaces between the cells. The protoplasm suffers a consequent coagulation which results in death. This appears to be the usual cause of death from freezing, although there may be others. In the cells with a high sugar content or with a more concentrated protoplasm ice forms less readily, and these plants, as a rule, withstand lower temperatures. Dormant seeds and the reproductive bodies of lower plants with low water content can, in some cases, withstand an indefinite amount of freezing.

An explanation offered for killing by high temperatures is the coagulation of the proteins in the protoplasm. It is a well-known fact that dry proteins require a higher temperature for coagulation than do those dissolved in water, and it is likewise true that dry seeds and other dormant parts will endure more heat than active, succulent ones.

Cardinal Points of Temperature.—Aside from danger to life, temperature exerts a marked influence on the physiological activities of plants—nutrition, chemical change, growth, reproduction, irritability, and movement. For each such activity there are for each kind of plant three cardinal points of temperature: (1) *the minimum* or lowest temperature, (2) the *maximum* or highest temperature, and (3) the *optimum* or most favorable temperature. Can a plant retain life at a temperature above the maximum or below the minimum for its physiological activities? Experiments show that it can, if the time during which it is exposed to that temperature is not too long. Time, then, is an important factor in determining what extremes of temperature, especially of heat, a plant can endure.

If we examine plants with a view to finding morphological structures that enable them to resist extremes of temperature, we meet with little success except in relation to water content. Evidently there are physiological or chemical differences between tropical and arctic plants that are yet to be explained.

Day and Night Requirements.—Greenhouse workers have observed that some species thrive at a higher temperature than others, but,

which is somewhat surprising, many plants require for their best development a night temperature a few degrees lower than the optimum for the daytime. Continuous growth at the optimum day temperature results in poor development of flowers and fruit, although the plants may appear otherwise healthy and produce vigorous stems and leaves.

No Temperature-Regulating Mechanism.—Birds and mammals develop considerable heat, resulting in body temperatures that may be quite different from those of their usual surroundings. They also have mechanisms which regulate their body temperatures. Not so with lower animals nor with plants. Probably all plants evolve some heat as a result of respiration, and considerable heat is absorbed from the sun, but ordinarily it is so quickly conducted away that no elevation of temperature is noticed. However, the flowers of some aroids, when opening, evolve heat so rapidly that they become distinctly warmer than the surrounding air, and large masses of germinating seeds, if insulated, develop a relatively high temperature. Even in these cases there is no temperature-regulating mechanism, such as is found in warm-blooded animals, to hold the temperature of the plant constant, regardless of the surroundings.

The evaporation of moisture from leaves has a cooling effect, but as they are usually very thin their internal temperature is determined by that of the surrounding atmosphere.

Effects of Dryness

When plants left their marine habitat and took up a terrestrial life they accepted a tremendous hazard. For the first time they faced the stern reality that "without water there can be no life." A submerged plant can absorb the oxygen and carbon dioxide dissolved in the surrounding water without the possibility of injury from evaporation. The aerial portions of terrestrial plants have never been able to accomplish this. Where the air enters the water escapes. The best compromise they have been able to achieve is to slow down evaporation and bring up a supply of water from the soil as fast as it is lost from the leaves. Some of the devices for reducing evaporation from leaves are shown in Figures 65, 66, and 67, pages 98, 99, and 100.

Xerophytic plants have a double battle to fight. On the one hand, the soil yields a scanty or intermittent supply of water, and, on the other hand, the dry air takes up water vapor from the leaves with great avidity. In actual fact the structural modifications of xerophytes, by

which they are able to survive in desert regions, are more in the nature of preventing evaporation from the leaves than of increasing absorption by the roots, although both are important.

Air Currents

Plants have adapted themselves to movements of the surrounding air so that, within reasonable limits, they are not injured by it. One effect of winds on growing herbaceous plants seems to be a stimulated development of mechanical tissues. Other conditions being equal, plants grown out of doors in the wind have tougher stems than those grown in the quiet air of a greenhouse.

Movements of the air are known to increase evaporation from the leaves, necessitating a greater water supply in the soil. This fact can be demonstrated in a quiet greenhouse by placing a vigorous potted plant on a balance and weighing it at intervals to determine the amount of water lost. If an electric fan is used to cause an air movement over the leaves of the plant and other conditions are not altered, the loss of water will be greater than when the air is quiet.

Continuous winds from one direction have a marked effect on the development of trees, causing the branches on the windward side to be shorter and fewer in number than those on the leeward side. Sometimes, also, there is a noticeable leaning of the trunk and bending of some of the branches away from the wind. This phenomenon has often been observed near the timberline of high mountains and in high mountain passes, and in some localities on the plains and along the seashore.

While the one-sided top is the most obvious effect of wind from one direction, it is not the only one. In some cases the bark of the trunk is relatively smooth on the exposed side and more rough and shaggy on the sheltered side. If such a tree is cut it is seen that growth in diameter has been less on the windward side than on the leeward side, giving the rings of growth an eccentric appearance. If the tree is dug up it is found that the roots have made the best growth on the side toward the prevailing wind, i.e., on the side opposite the longest branches.

There is little doubt that the smoothness of the bark on the side toward the wind is due to abrasion by wind-blown particles, but the explanation of the unequal growth of branches, trunk, and roots is not so certain. Probably some damage is done to the buds at the tips of the branches exposed to the wind, which retards, and in some measure prevents, the development of branches on that side. On the leeward

side the branches are subjected to more or less pull, and under experimental conditions it has been shown that such a strain stimulates growth in length, but this is of minor importance, as these branches are but little longer than those of normal trees. As for the roots, pressure against the top would naturally cause some pull on those growing on the windward side when the ground was soft from rains or from thawing. The

FIG. 34. Coniferous trees on Mount Rainier, distorted by wind from one prevailing direction. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

relatively poor growth of the trunk on the windward side, resulting in narrow annual rings, may be due to an inadequate food supply from the weak and scattering branches above.

REVIEW QUESTIONS

1. State the advantages that terrestrial plants have over submerged plants.
2. State the disadvantages that terrestrial plants encounter, not shared by submerged plants.
3. What visible changes take place in a plant if placed in darkness and kept there?
4. *How does light intensity affect the rapidity of elongation in the stem?*
5. Explain the greater height of trees in a dense forest than that of the same kind and age growing in a field.
6. By what means are plants able to obtain the maximum amount of exposure to the light?
7. How does the intensity of the light affect the strength of the stem?

8. What is the usual effect of light on the germination of seeds?
9. About what is the extreme range of temperature for the development of plants?
10. In what two general ways are plants affected by adverse temperatures?
11. Which are subject to greater fluctuations, air temperatures or soil temperatures?
12. What is meant by cardinal points of temperature?
13. Do plants generate heat? Evidence?
14. What is the effect on a plant of keeping it constantly, day and night, at the optimum temperature for daytime growth?
15. How do higher plants compare with higher animals in the matter of temperature-regulating mechanism?
16. Why does a terrestrial plant need to have pores in the leaves, that permit the escape of moisture?
17. Give evidence that air currents stimulate the production of strengthening tissues in a plant.
18. What is the effect of air currents on the evaporation of moisture from the leaves?
19. Explain the effect on trees of a continuous wind from one direction.
20. Why does the stem of a land plant need to be more rigid than the stem of a plant submerged in water?

PART THREE

PLANTS AND THEIR FOOD

CHAPTER V

CELLS, THE UNITS OF STRUCTURE

As a preliminary to studying the great subject of plant nutrition, it will be necessary to learn something about the living portion of the plant that needs to be nourished and something about the workshop for the manufacture of the necessary foods within the plant.

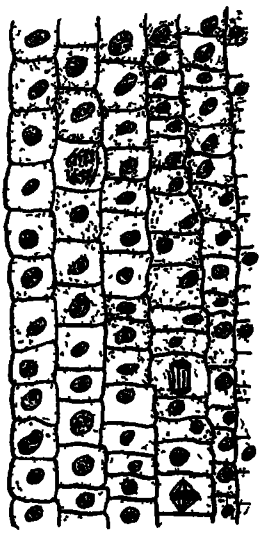


FIG 35 Longitudinal section of the growing portion of a young root, showing it to be made up entirely of cells

In all our studies we find nothing more remarkable than living protoplasm, the origin of which is still a subject of speculation But even though its origin is unknown, much of value has been learned concerning it. If we cut a thin section of any part of a plant or animal we find it made up of innumerable microscopic boxes of protoplasm that have received the name *cells*. These cells are more conspicuous in plants than in animals because of their more definite walls; otherwise they

appear much the same. Each cell constitutes a unit in the structure of a plant and is, in itself, a very complicated bit of mechanism. A general knowledge of it is easily acquired, but an extensive consideration is far beyond the scope of this chapter and constitutes the subject of *cytology*.

We have learned that living things require food, grow, reproduce their kind, and are sensitive to changes in their environment. The liv-

FIG. 36. Branch of a small, aquatic, flowering plant, *Elodea*, which is especially suitable for the study of living cells.

ing cells carry on all these activities, and different parts of the cell, or *cell organs*, have become specialized to do different things.

A Representative Plant Cell.—One of the most favorable plants for a first study of cell structure is the little, aquatic, flowering plant, *Elodea*. In this plant the leaves are small, only two cells in thickness except at the midrib, and so transparent that the internal structure can be readily seen with a microscope. When a satisfactory cell for study has been selected, a considerable differentiation of parts can be seen.

Around the outside, completely enclosing the living portion, is a thin, transparent *wall* of secreted material—not protoplasm. Within it, and filling the entire space, is the *protoplast*.[1] This is the unit of life, and

[1] Many students find difficulty in distinguishing between the terms "protoplast" and "protoplasm." The protoplast is the cell exclusive of its wall, with the cell organs normally placed. Protoplasm is the material of which the protoplast is made—cytoplasm, nucleus, etc.

it is made up of protoplasmic materials of various kinds definitely arranged. The outer layer of the protoplast is an extremely thin *plasma membrane* closely adhering to the wall. This membrane aids in regulating the intake of food materials. If thickening of the wall becomes necessary, new material for this purpose is secreted from this membrane.

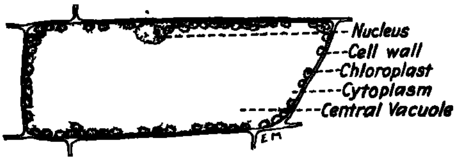


FIG. 37. Single cell of *Elodea* leaf, showing the various cell organs. Note that the central vacuole occupies a large part of the space.

FIG. 38. Sectional view of a chloroplast, showing the peripheral chlorophyll-bearing layer. Diagrammatic.

There is evidence that in some cells it is the part that is sensitive to stimuli. The plasma membrane is the outer part of the *cytoplasm*, a semi-liquid, colloidal material that occupies a large part of the cell. It has much to do with food manufacture and with the growth of the cell. There are also some tiny, oval plastids that are carried about in the currents of cytoplasm. If these plastids are green they are called

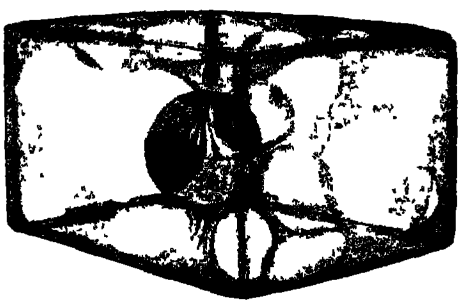


FIG. 39. Perspective view of a young cell showing cell organs in place. Somewhat diagrammatic.

chloroplasts and are of vital importance to the welfare of the plant. They contain the pigment, *chlorophyll*, characteristic of all green plants. By utilizing energy from the light of the sun, they are able, with the aid of the cytoplasm, to manufacture sugars and starches from carbon dioxide and water—something that animals cannot do. Embedded in

the cytoplasm is a denser, rounded body, the *nucleus*. It is an important organ in reproduction, as it is responsible for transmitting heredity

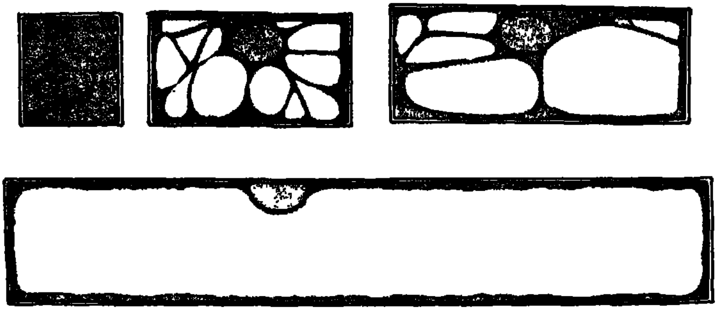


FIG. 40. Cells from red-top grass, illustrating the changes that take place as they mature. Note that the large central vacuole is formed by the union of smaller ones. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

traits from parent to offspring. Within non-reproductive cells, it seems to regulate to some extent various activities such as the absorption of food materials, and perhaps growth. A considerable proportion of the center of the cell is occupied by a *central vacuole* containing non-living materials—water, with dissolved mineral matter, a little sugar, etc.

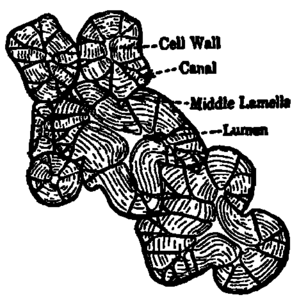


FIG. 41. Stone cells from the shell of English walnut. Note the thickness of the walls. (*Reprinted by permission from Textbook of General Botany*, Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc.)

New Cells from Old.—If all plants and parts of plants are composed of cells, it is evident that a large mature plant must contain either

much larger cells than the tiny young ones or many more. Actually, cells do increase in size after their formation, and large plants contain vast numbers of them. Where did they all come from? There is an

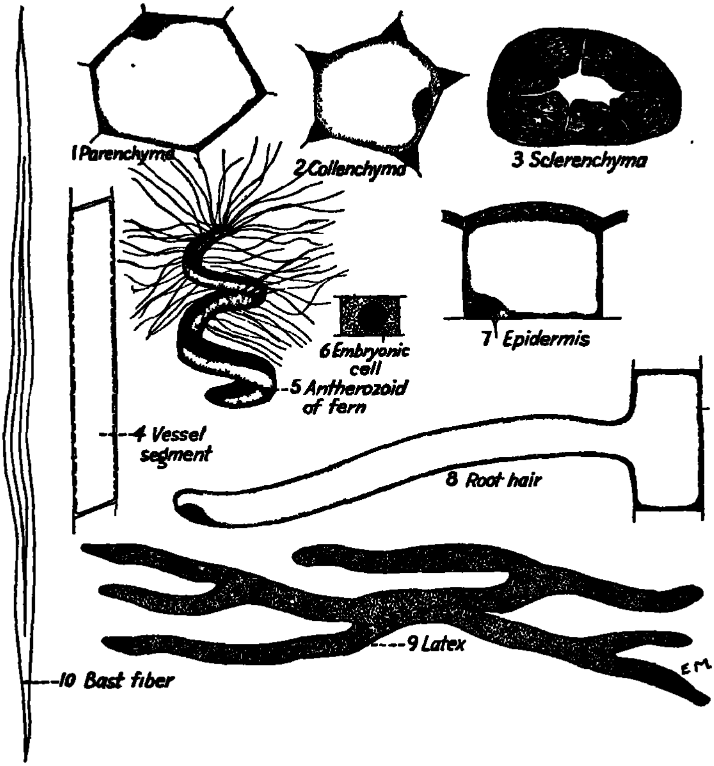


FIG. 42. Mature cells that have become specialized to carry on various functions. Changes in size, shape, thickness of wall, and formation of central vacuole have taken place.

old dictum, "Every cell from another cell." To be specific, cells already existing divide to form new ones. The older one is called a *mother* cell, and those that result from the cell divisions are called *daughter* cells.

As a rule each cell has at first a single nucleus. This divides to form two, and then a new wall is built across the cell between these two nuclei, dividing it into two daughter cells.

Nuclear division and cell division are intricate processes that will be described in detail in Chapter XI.

Specialization of Cells.—Young, newly formed cells are relatively small, thin-walled, and densely filled with protoplasm, no central vacuole being yet formed. In specialization of parts and division of labor a considerable variety of cells is needed. They become specialized as they

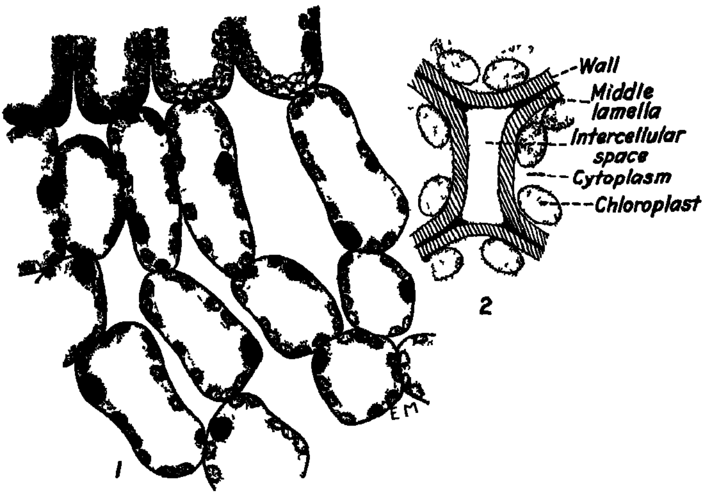


FIG. 43. Intercellular spaces in the tissues of an apple leaf 1, the fully developed spaces; 2, the method by which the walls of adjacent cells round up and separate, leaving an air space.

grow older and take up their several duties. Their growth is usually accompanied by the formation of a central vacuole. Sometimes the walls become thick and hard, as in the shells of nuts, in peach pits, etc. Some of them elongate and develop thick walls, as in the tough fibers of bark. Others elongate and also increase in diameter, lose their protoplasm, and become tubes for the conduction of sap. In some cases the walls remain thin, but the cells enlarge and serve for food storage. It will be seen, then, that in the specialization of cells these changes may take place: (1) enlargement, (2) change in shape, (3) thickening of walls, and (4) development of central vacuoles. Not infrequently, during the changes in shape and size, the cells separate from each other in places, especially becoming rounded at the corners, so that *intercellular*

spaces are formed and filled with air. These spaces are often continuous with each other and make possible a circulation of air through the plant. Thus, by utilizing different combinations of specialized cells, all the complicated organs of a plant are produced, and the performance of many kinds of work is made possible. When it is remembered that everything a plant can do is made possible by the combined action of its cells, the importance of cytology and histology, which deal with cells both young and mature, will be appreciated.

Review Questions

1. What name is used for the materials that make up the living parts of a cell?
2. What branch of biology deals with the detailed structure and the physiology of cells?
3. List the organs of a typical plant cell, state where each is found, describe the appearance of each, and give the functions of each.
4. What parts of the cell are living? What parts are non-living?
5. Distinguish between the words "protoplasm" and "protoplast."
6. Describe the appearance and the habitat of *Elodea.*
7. What is in the central vacuole of a cell of *Elodea?*
8. By what means do cells increase in number?
9. What is meant by intercellular spaces?
10. How do they form?
11. What do they contain?
12. As cells mature, what morphological changes most commonly take place in them?
13. Why are cells often spoken of as "units of life" and "units of structure"?
14. As the cells of a plant enlarge they commonly develop large central vacuoles. Why would it not be just as well for the plant to fill this space with cytoplasm?
15. Why do botanists go to the trouble of securing *Elodea* instead of using the leaves of more common plants for a study of living cells?

CHAPTER VI

CONTRIBUTIONS OF AIR AND SOIL

Plants in their nutrition make use of the simplest of raw materials. It does not require much training in chemistry to know that water and carbon dioxide are simple substances, and the composition of such salts as potassium nitrate, calcium phosphate, and magnesium sulfate is easily comprehended. Yet these substances and closely related ones make up the greater part of the food materials for most green plants. But it is a far cry from carbon dioxide to protoplasm, and the fact that a plant can build such a complex substance from such crude materials places it in the first rank as a manufacturing chemist.

Food Requirements of Plants.—One method of learning the needs of a growing plant is to determine its composition. If we dry a sunflower plant it loses about eighty per cent of its weight. Of the remaining dry matter, one of the most abundant elements is carbon, a fact which explains the blackening when wood is charred by heat. Cytoplasm is very rich in nitrogen, and nuclei are high in phosphorus. For the formation of chlorophyll a trace of iron is necessary, although this element does not enter into its composition. Altogether the following ten elements are necessary: carbon, hydrogen, oxygen, nitrogen, potassium, phosphorus, sulfur, calcium, magnesium, and iron. A few other elements are beneficial to certain plants. This seems like a formidable list of materials to be secured by plants with no power of locomotion, but they succeed; otherwise there would be no plants. The first four named—carbon, hydrogen, oxygen, and nitrogen—are used in the greatest abundance, but it is not correct to say that they are the most important, for all are essential.

THE AIR, A STOREHOUSE OF FOOD MATERIALS

For a long time attention has been focused on the soil as a source of food for plants, largely because of the struggle man has had to maintain soil fertility. The work of the last two centuries has shown, however, that, aside from water, plants obtain more food materials from the

air than from the soil. Because this food exists in a gaseous state and because the supply is reasonably constant, we have not given it the attention that it merits.

Composition of the Air.—The air varies slightly in composition under different conditions, but it always contains certain ingredients. In the following list the approximate proportions are given by volume.

Nitrogen	78.0%
Oxygen	21.0%
Argon	.94%
Carbon dioxide	.03%
Hydrogen	trace
Water vapor	variable
Impurities	variable

Water vapor is the most variable of the normal constituents of air. The amount depends on two factors: (1) the supply that is available from evaporating surfaces and (2) the temperature, warm air holding more than cold air. In cold, dry air there may be less than 0.1 per cent, while in hot, damp regions there may be as much as 5 per cent. While the range of variation in *total* or *absolute* humidity is here given on a percentage basis, it has been found more significant to determine the *relative* humidity, i.e., the degree of saturation of the air with water vapor. A given amount of water, say 0.5 per cent, represents low relative humidity in warm air and high relative humidity in cold air.

Something should be said about the presence of hydrogen in the air. This gas is released into the air in small quantities as a product of decay brought about by bacterial action, and this process has been going on for a very long time. Hydrogen is a very light gas and tends to rise away from the earth. However, the different gases are mingled with each other by diffusion and by air currents instead of covering the earth in layers according to their weight. There is evidence that there are minute traces of hydrogen throughout the atmosphere, but not so much as would be expected as a result of accumulation through the ages. At ordinary temperatures this hydrogen would not unite with the oxygen of the atmosphere, and it is so dilute that fires would not cause extensive oxidation of it. The suggestion has been offered that a little may be oxidized by ozone released by electric discharges, and it seems quite likely that some of the hydrogen reaching the outer portion of the stratosphere may go farther and be lost in space.

Sources of Gases in the Air.—Leaving out of consideration the original sources of our atmosphere before life appeared on the earth, we

face the fact that some of the gases of the air are constantly being used by plants and animals and are as steadily being replaced. Carbon dioxide is formed and released into the air by combustion—forest fires, the burning of fuels, gasoline, etc.—by the respiration of animals and plants, and by certain processes of fermentation and decay. Volcanoes also discharge some carbon dioxide. The waters of the ocean contain much more of this gas than does the atmosphere. When warm they release it, and when cold they absorb it. Thus the percentage in the air has varied through the ages. Oxygen is released from green plants during the daytime as a by-product of food manufacture. When plants first appeared on the earth there was very little of this gas in the atmosphere. The action of green plants is responsible for the high percentage that now exists. Nitrogen is released into the air through the decomposition of nitrates by certain bacteria. Water vapor escapes from the leaves of plants and from bodies of water and moist surfaces everywhere.

Withdrawal of Gases from the Air.—The composition of the air now remains fairly constant. As fast as gases are added they are removed by other processes. The carbon dioxide is used in photosynthesis by green plants. The oxygen is used in respiration by animals and plants and is consumed in the burning of combustible materials. Higher plants cannot use nitrogen in the free state but a few species of bacteria remove it from the air and "fix" it in the form of compounds that can serve as food to most kinds of plants. Appreciable quantities are also fixed by electric discharges. Man has devised processes by which some nitrogen is recovered from the air in the form of compounds. Water is precipitated from the air in the form of rain and snow, practically none in the gaseous condition being taken up by the plants.

It has already been noted that free hydrogen does not exist in the air to any appreciable extent, but even if it did plants could not use it for food.

Materials Secured by Plants from the Air.—It has already been learned that the air contains carbon dioxide. Even though it contains only 0.03 per cent, the air furnishes practically all the carbon used by the plant, in which it forms a large proportion of the dry weight. There is some evidence that the percentage of carbon dioxide in the air was once much higher than now, and experiments show that a higher percentage is beneficial to most plants. Nevertheless this small amount suffices because of the great efficiency of the leaves in collecting it (see page 107). Oxygen, likewise, is taken chiefly from the air, but some is obtained from compounds in the soil. Although the leaves are bathed

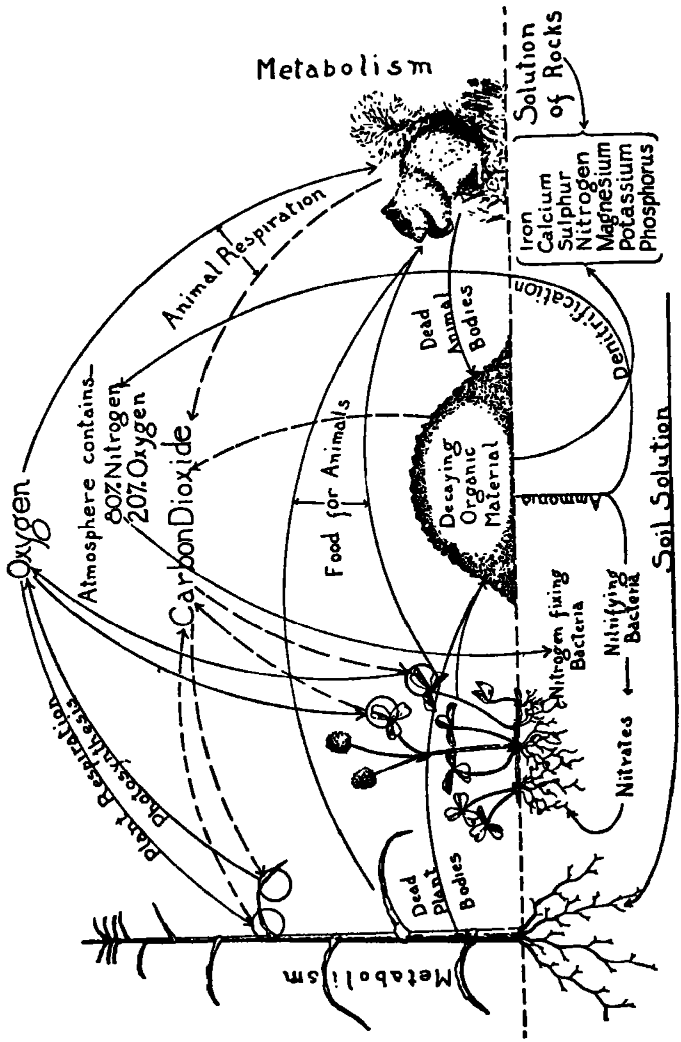


FIG. 44. Diagrammatic representation of the processes that result in chemical changes in the air and soil. (From Eyster's *College Botany*, Farrar & Rinehart.)

constantly in nitrogen, the most abundant gas in the air, they are unable to use it in that form because of its chemical inertness, i.e., the difficulty of making it combine with other elements. Moisture cannot be absorbed from the air by the leaves to any great extent, although they benefit by its presence there because it lessens evaporation.

Soil, the Source of Water and Minerals

From the soil plants obtain practically all their supply of water, which makes up a large part of their weight in the living condition. There is a difference of opinion as to the amount of carbon taken from the soil by the roots of plants. Apparently they absorb a little in the form of carbonates and carbonic acid, but certainly the greater part of the carbonaceous material enters the leaves as carbon dioxide from the air. From the soil they also obtain mineral salts containing potassium, phosphorus, nitrogen, calcium, magnesium, sulfur, and iron. Relatively small amounts of these are used but they are absolutely essential to the life of the plant.

Especial mention should be made of those food elements of which there is too frequently a shortage. These are potassium, phosphorus, and nitrogen. The last named occurs in the free state in the air and is an ingredient of a considerable number of both organic and inorganic compounds. Nitrates and ammonium salts are the ones chiefly utilized by higher plants. Probably the majority thrive best on nitrates, but ammonium salts are preferred by rice and some others. Ammonium salts are rather unstable in the soil, being readily changed to nitrates by certain bacteria, and hence they are generally much less abundant than nitrates.

Air versus Soil.—It will be profitable to compare the contributions of air and soil to the nutrition of plants. In the composition of the dry matter of plants, oxygen and carbon are the most abundant elements. They are, indeed, more abundant than all others combined. Air furnishes practically all of the carbon and considerable of the oxygen. It, therefore, must be credited with supplying much more of the dry matter of plants than does the soil.

As for water, a small portion is used for the manufacture of food, especially of carbohydrates, and for the building up of protoplasm, but it largely serves to carry dissolved food from place to place and to keep the plant erect and turgid, i.e., free from wilting. Thus only in part can it be classed as a food material, for it serves other purposes as well.

Maintenance of Fertility.—The fertility of the air presents no problem to man. The supplies of carbon dioxide and oxygen are maintained by natural processes. With few exceptions soils contain ample quantities of hydrogen, calcium, magnesium, sulfur, and iron. Therefore the conscious efforts of man in maintaining soil fertility are concentrated on supplying potassium, phosphorus, and nitrogen. For the most part compounds of these elements, having been removed from the soil by growing plants, are returned to the soil again as the plants die, or in the manure or the dead bodies of animals that have eaten them. Inevitably, however, some of these materials are removed and transported elsewhere.

Potassium is restored to the land chiefly in the form of potash fertilizers, or, to a limited extent, in wood ashes. Great potash beds are found in Germany, and there are a number of small ones in the United States. Recently very extensive deposits have been opened up near Carlsbad, New Mexico, which might become the chief source of potash for this country were it not for the heavy cost of transportation to the eastern fertilizer factories.

Phosphates occur in extensive deposits throughout the Rocky Mountain region. Other deposits are found in the southeastern states, and these can be shipped more cheaply to the eastern fertilizer factories.

The problem of supplying nitrates is not so simple. Enormous amounts have been deposited as saltpeter, chiefly sodium nitrate, in northern Chile and this is shipped to other countries. However, much of the nitrate used in the United States is manufactured by chemical processes. Ammonium salts, chiefly ammonium sulfate, are now produced in this country as by-products in the manufacture of coke or of producer gas. The nitrogen in this form is not suitable for the use of most higher plants, but when it is added to the soil certain nitrifying bacteria (see page 224) change it rapidly into nitrates. Of still greater importance in the restoration of nitrogenous compounds to the soil is the action of certain kinds of bacterial organisms. These bacteria have the rare power of utilizing the nitrogen existing in the air in the elemental state (free nitrogen) and changing it into compounds useful to themselves and, incidentally, to other plants and man.

Nitrogen Fixation.—This process of combining free nitrogen with other elements is called *nitrogen fixation*. Its value is incalculable to all plant and animal life. There is a tendency for the nitrogenous compounds in the soil to be changed so as to release nitrogen into the air and thus deplete the supply to a degree that would make the earth unin-

habitable for plants and leave the animals to starve. This tendency is successfully overcome by nitrogen fixation, the greater part of which is brought about by the action of a few species of bacteria.

Two methods are known by which these bacteria fix nitrogen. One kind of bacteria lives in the soil, takes up nitrogen gas from the air spaces, and, by some unknown means, combines it directly with other elements. This process goes on in soils practically everywhere, whether the land is cropped or fallow.

The other kind of bacteria lives a hazardous life in the soil until the land is planted to a leguminous crop, as peas, beans, clover, or alfalfa. Then these bacteria attack the roots, behaving as though they were parasites and stimulating the formation of many tiny galls, or *nodules* (see page 225). Inside these nodules the bacteria live, and, taking up nitrogen in the free state from the soil, convert it into nitrogenous compounds. This kind of bacteria fixes nitrogen much faster than the other if leguminous plants are available, but if the land is fallow or planted to a non-leguminous crop their action is negligible. This subject is further discussed in Chapter XVII.

Review Questions

1. If a herbaceous plant is weighed, dried, and reweighed, will the dry weight be more or less than half the original weight?
2. If the dry matter is burned, will more or less than half be left as ash?
3. Of the three portions, water, combustible dry matter, and ash, which came chiefly from the soil and which from the air?
4. Name the ten chemical elements required by all green plants in their nutrition.
5. Which four of these are used in greatest amount?
6. In what combination or form is each of the following elements usually taken by plants: (1) potassium? (2) phosphorus? (3) nitrogen? (4) oxygen? (5) carbon?
7. Which chemical elements are obtained by higher plants almost exclusively from the soil?
8. Which are obtained almost exclusively from the air?
9. Name one that is obtained in considerable quantity from both soil and air.
10. Does the air or the soil contribute most to the weight of a growing plant?
11. Does the air or the soil contribute most to the dry weight of a plant?
12. Which of the chemical elements are most likely to occur in insufficient quantity for the plant?
13. State the approximate percentage composition of the air.

14. Explain how each of the following is withdrawn from the air: (1) oxygen, (2) carbon dioxide, (3) nitrogen, (4) water vapor.
15. Explain how the air is kept supplied with each of these gases.
16. In plant physiology what distinction is made between food materials and foods? Which are chiefly organic and which inorganic?
17. Name five of the most important food materials.
18. Name two of the most important foods.
19. What is the distinction between "relative humidity" and "absolute humidity"?
20. Does warm air or cold air contain the more water vapor when saturated?
21. Does warm water or cold water contain the more carbon dioxide when saturated?
22. Give the chief sources of the following for the United States: (1) nitrates, (2) phosphates, (3) potash.
23. What is meant by nitrogen fixation?
24. Name two agencies that carry on nitrogen fixation in nature.
25. Explain why the air in the soil spaces contains a lower percentage of oxygen and a higher percentage of carbon dioxide than that aboveground.
26. What is the distinction between relative humidity and absolute humidity?
27. Under what conditions would each of the following exist: (1) high *relative humidity with low absolute humidity?* (2) low *relative* humidity with high absolute humidity?
28. Under what conditions could the roots of a plant be in a relatively dry soil without the leaves wilting?

CHAPTER VII

ABSORPTION AND TRANSFER

Plants, like animals, have to get water and nutritive materials to places in their bodies where they are needed and must get rid of waste products that are undesirable or even harmful. That these ends are accomplished in higher animals largely by the movement of blood and lymph is well known. Plants, however, are without a true circulatory system, and yet they need to transport materials to and from all living cells.

Given a supply of carbon dioxide and oxygen in the air outside the plant, and a supply of water and mineral food in the soil outside the plant, how does it collect these, bring them together, and combine them into the complex organic materials of its body? Having manufactured carbohydrates in its leaves, how are they transported to all living parts of the plant and to storage organs? To explain these things we enter into some of the most interesting and instructive chapters of botany.

As the cells of the young roots and the root-hairs present no openings, it might seem impossible for the soil water to gain access. That it does enter them is certain, and how it enters them will now be explained.

Diffusion and Osmosis.—To make the processes more clear four simple experiments will be described. (1) If ammonia gas is released in a room where the air is quiet, within a very short time the odor will penetrate to the farthest corner. The molecules of the ammonia move in all directions until the chemical is evenly distributed throughout the room. That is, the ammonia gas has *diffused* through the air of the room.

(2) If a glass is partly filled with water and a small lump of sugar is dropped into it, the sugar will dissolve. As it does so it slowly diffuses in all directions. Diffusion is most rapid from the region of the greatest concentration of a substance in solution to that of the lowest concentration of that substance. Correspondingly, the water will diffuse into the region where the sugar is most plentiful and water is scanty. These diffusions will continue until the water and sugar are evenly distributed through each other. If a third substance, such as common salt,

is placed in the same glass of water and sugar, it will also diffuse until all three are equally distributed. Furthermore, diffusing substances may meet each other and pass in opposite directions at the same time with little or no interference. The explanation of diffusion here used is based on the evidence that molecules in a gaseous state or in a solution are in active motion and tend to scatter in all directions.

(3) In the third experiment a suitable membranous sac containing a strong solution of sugar is submerged in a glass of pure water. It might seem as though the membrane would keep the sugar from diffusing out into the water and the water from diffusing through into the sugar solution, but such is not the case. In time the two substances will be evenly mixed. The phenomenon of diffusion of substances through a membrane is termed *osmosis*. A point to remember is that each substance passes through from the place where it is more concentrated to the place where it is less concentrated. Also, the passage of the two substances, water and sugar, through the membrane in opposite directions is simultaneous.

(4) A fourth experiment is somewhat like the third, but the sac in this case is made of a *semi-permeable* membrane, one that the water can pass through readily but the sugar cannot. In this case the sac contains a strong sugar solution and the glass in which it is placed contains pure water. Because of the nature of the membrane the sugar is unable to pass through, but the water diffuses from the place where it is pure through the membrane to the interior of the sac where there is only a little in proportion to the concentration of sugar. Naturally the sac will thus become fuller than it was at the beginning of the experiment.

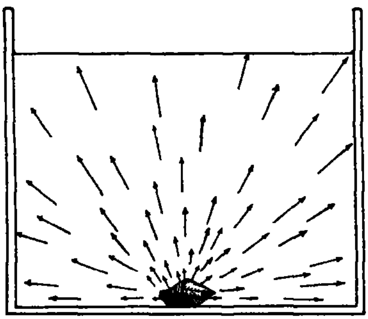


FIG. 45. Diagram illustrating the diffusion of sugar in water, from a lump where it is concentrated to regions where it is less concentrated.

In its simplest form osmosis is not difficult to understand. However, the impression must not be gained that the water flows through the membrane carrying the chemical with it. This supposition has led many students into error. Each substance, even though there be a considerable number, diffuses through independently of the others and of the passage of the water. Furthermore, it should be stated that the character

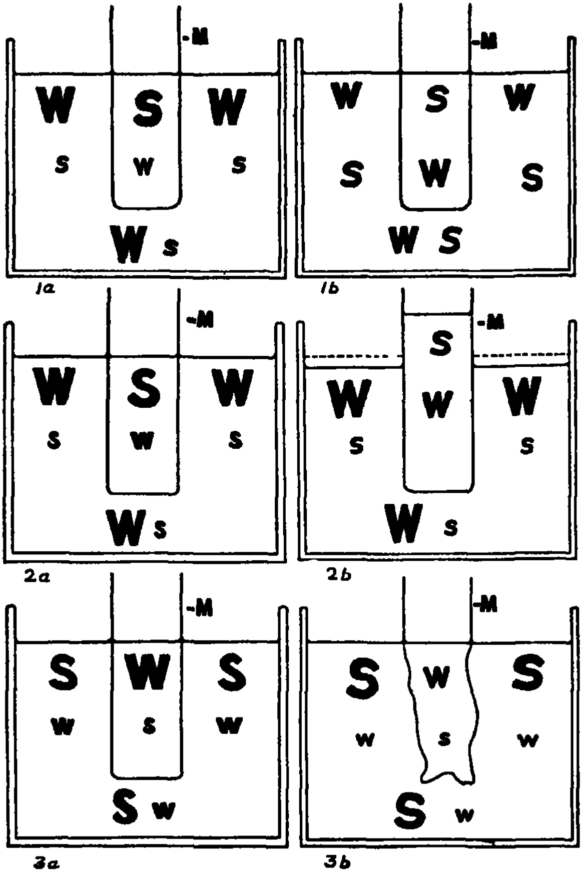


FIG. 46. Diagrams of three experiments illustrating the passage of water, W and sugar, S, through a membrane, M, by osmosis. The concentration of the substances is indicated by the size of the letters. Each tends to pass from the side of the membrane where it is more concentrated to that where it is less concentrated. In 1a the membrane is permeable, permitting the passage of both water and sugar. Water will pass into the membranous sac, and sugar will pass out of it until a condition of equilibrium is reached, as in 1b. In 2a the membrane is differentially permeable, permitting the passage of water but not of sugar. Therefore, the water will enter the sac where its concentration is low, causing a rise in the column as shown in 2b. In 3a, likewise, the membrane is differentially permeable, and the water will pass out of the sac where it is concentrated into the surrounding liquid where it is rare. As a result the sac will collapse as in 3b.

of the osmotic membrane determines to some extent what substances can pass through and what substances are held back. For example, alcohol passes through a rubber membrane much more readily than does water, provided the membrane is wet. Indeed, some chemicals cannot pass at all through any membrane. As a rule, a substance must be dissolved in order to pass through an osmotic membrane. Sugars, and many salts and acids, readily dissolve in water and diffuse through membranes of various kinds. Some materials exist in water, not as true solutions but as particles in suspension. They are larger than molecules but

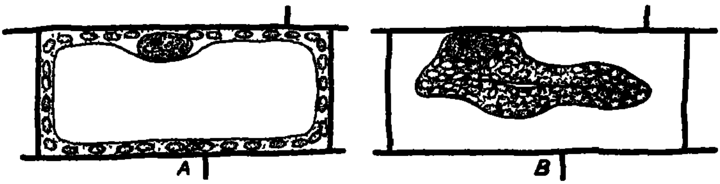


FIG. 47. Plasmolysis of *Elodea* cell. A, living cell in normal condition. B, cell that has been immersed in a strong solution of common salt, which has caused most of the water to pass out of the central vacuole by osmosis. As *the plasma membrane, rather than the cell wall, is the osmotic membrane*, the wall has held its shape, while the protoplast has collapsed inside it. B, somewhat diagrammatic.

yet too small to be seen with the microscope. These substances, suspended in water or other liquids, form *colloids*. Proteins, gelatin, etc., mingled with water are colloidal. Colloidal particles are less active than are molecules in solution. On that account and because of their larger size they fail to pass through membranes by osmosis.

Plasmolysis of Cells.—If we substitute plant cells for the simple apparatus just described, the same principles hold. The plasma membrane next to the cell wall and the protoplasmic membrane around the central vacuole are semi-permeable. Pieces of living plant tissue such as beet root if placed in a strong sugar solution will shrivel. Why? The cell sap of the beet, having a higher percentage of water than the sugar solution, passed out through the membranes and was not replaced by the sugar. The cells collapsed as a result. Cells that give up their water and shrivel because of such treatment are said to be *plasmolyzed*. In most plasmolyzed cells the protoplast has separated from the cell wall and collapsed inside it, showing that the plasma membrane, not the cell wall, was osmotic. Passage of water through the walls is aided by imbibition, described below.

If through the agency of osmosis, as when tissues are placed in distilled water, the cells become exceedingly full, they are said to be *turgid*. When applied to large organs, such as leaves and young succulent stems, turgidity enables them to stand erect and is in contrast to the condition of wilting.

Imbibition.—There is another process that aids in the movement of water. Some substances, like pieces of dry gelatin, that are hard and show no visible holes or pores readily "soak up" water. The water is attracted into spaces too small to be seen even with a microscope, and, forcing the particles of the solid apart, causes it to swell, sometimes with great force. It is largely by this process of *imbibition* that water passes into cell walls.

Role of Osmosis in Plants.—We have now seen methods whereby water and food materials can pass by imbibition into cell walls and by osmosis through plasma membranes into living cells. No processes are more essential to the life of the plant. Water and dissolved minerals thus pass into root-hairs and roots, and carbon dioxide and oxygen diffuse through pores into the leaves, where they become dissolved in films of moisture on the cell walls and enter there. These materials are also transported from cell to cell within the interior of a plant, passing, in general, from places where they are more concentrated to other places where they are less concentrated. Protoplasmic membranes are semipermeable, or *differentially* permeable, i.e., they restrain some substances and permit others to pass through. Furthermore, there is evidence that the membranes of certain cells change their permeability under different conditions, sometimes very quickly. Thus osmosis and imbibition regulate the turgor of the cells, aid in growth, and contribute to most of the plant movements described in Chapter II.

Mechanism for Transporting Water and Foods

Osmosis explains the entry of water and dissolved minerals into the roots and the entry of carbon dioxide and oxygen into the cells of the leaves. A third necessity lies ahead—that of getting these materials together. Most of the food manufacture is carried on in the leaves. They get certain raw materials from a near-by source, the air, but others have to be transported from the soil a considerable distance away. In the tallest trees this may be several hundred feet. To understand methods of supplying a factory we must know something of railroad systems,

highways, and steamboat lines. To appreciate the transport of foods within a plant we must examine its structure.

Root Structure.—Some knowledge of the structure of cells has already been gained from Chapter V. It will now be necessary to learn how these cells are arranged and specialized for most effective service.

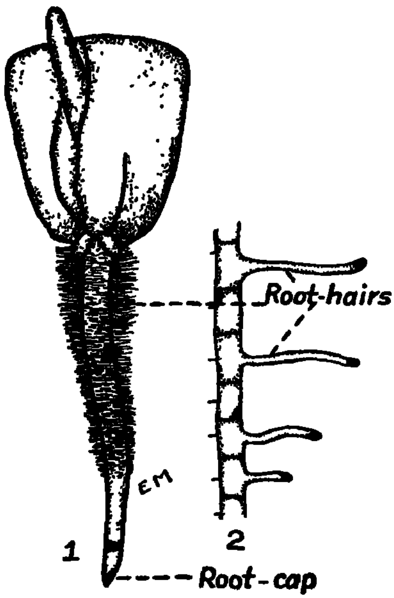


FIG 48. Root-hairs with osmotic membranes through which water and food materials enter the plant. Note that the nuclei have migrated into the root-hairs.

If we examine a cross section cut about one-fourth of an inch from the tip of a young root of a sunflower, we find on the outside a layer of cells, the *epidermis*. Certain epidermal cells extend outward, forming numerous *root-hairs*.[1] Each root-hair consists of a long, slender, thin-walled extension of an epidermal cell with cytoplasm, a nucleus, and a central vacuole. The root-hairs occur in a region just back of the root tip, and as new ones form on the younger portion the old ones wither

[1] The number of root-hairs on plants is astonishing. It has been estimated that a single winter rye plant produces approximately 14,000,000,000 with a total length of over 6,600 miles, and a surface area of about 4,320 square feet.

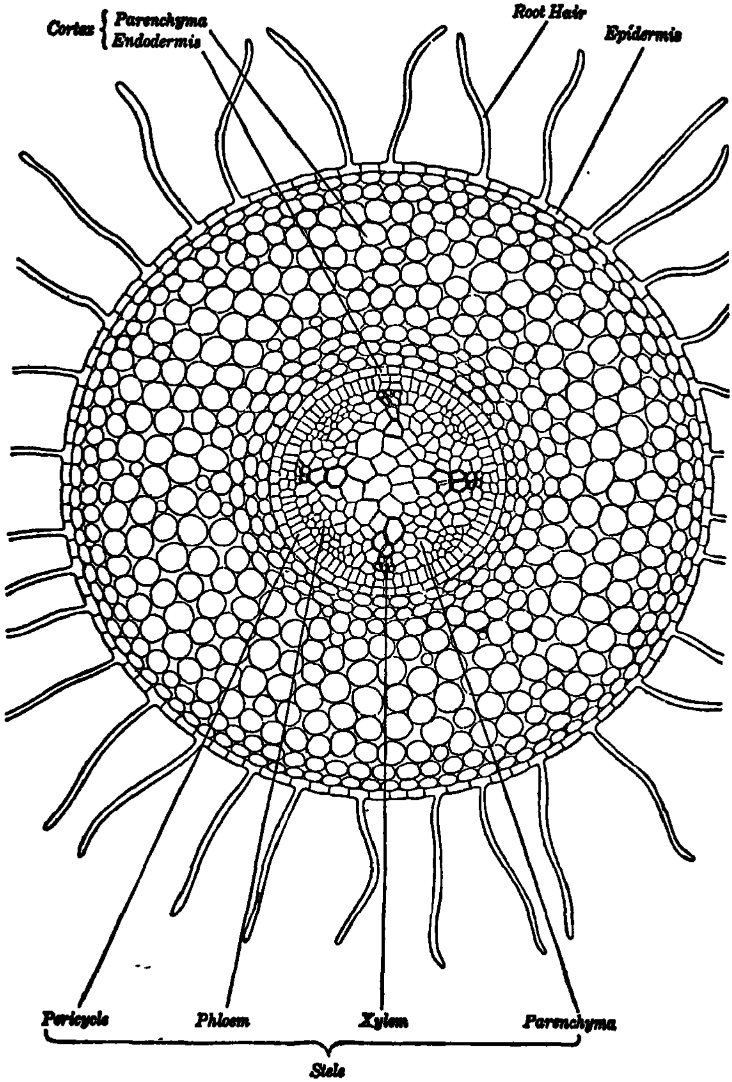


FIG. 49. Cross-section of a young root of a sunflower. (From Smith, Overton et al., *A Textbook of General Botany*, The Macmillan Company.)

away. Within the epidermis at this distance from the root tip the cells are essentially alike, for little differentiation has as yet taken place.

A cross section cut a half inch from the tip, where the root-hairs are old and withered, shows a more differentiated structure. Just in-

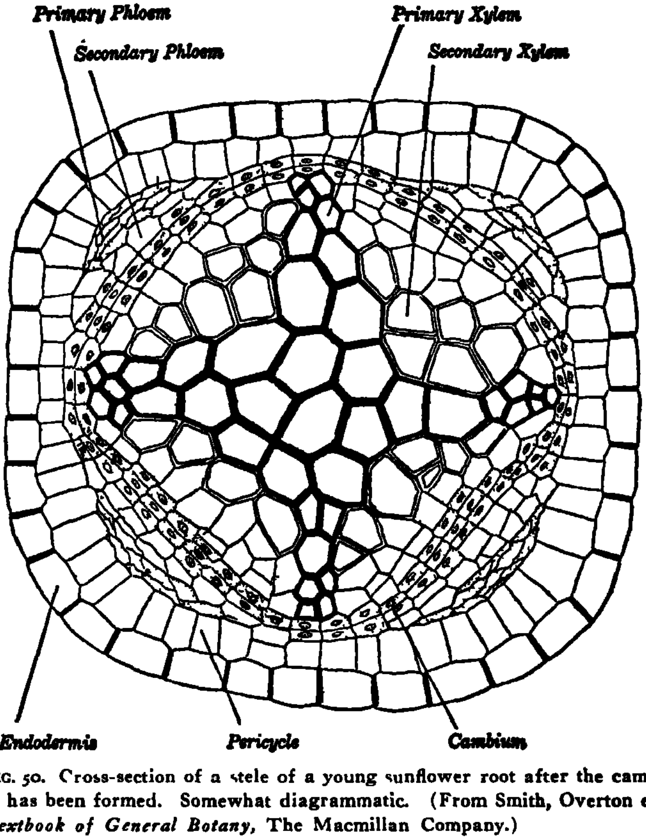


FIG. 50. Cross-section of a stele of a young sunflower root after the cambium layer has been formed. Somewhat diagrammatic. (From Smith, Overton et al., *A Textbook of General Botany,* The Macmillan Company.)

ward from the epidermal layer is the *cortex,* the inner cell layer of which is the *endodermis,* where in most plants there is a more abundant supply of starch grains than in adjacent cells. Within the cortex, as a core occupying the remaining central portion, we find the *stele.* It, in turn, has several distinct parts. The outer layer of cells is the *pericycle.* Just inside of this layer are bundles of cells elongated in the direction

of the long axis of the root. These *fibrovascular bundles* [1] are arranged in a layer around the center. In a very young sunflower root there are usually four *phloem* bundles in a circle near the pericycle. Four *xylem* bundles lie between the phloem bundles but are larger and extend from the pericycle to the center of the root. Separating the phloem region from the xylem region is a *cambium layer* of cells. Many plants

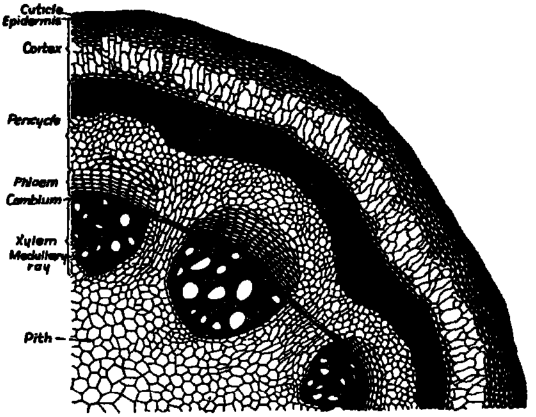


FIG. 51. Sector from cross-section of young stem of Dutchman's pipe—a dicotyledonous vine.

develop a *pith* in the center, but this is not present in the sunflower root.

Stem Structure.—If we examine a cross-section of an internode a few inches below the top of the stem, an arrangement of cells will be seen similar to that just described for the root but with a few important differences. There is an epidermis, a cortex, and a stele, but the arrangement of the phloem and xylem is somewhat different. The phloem is directly outside the xylem and the two are so closely associated that the pair form one bundle.

This young stem has a much greater diameter than that of a rootlet of the same age and contains a larger number of fibrovascular bundles. The pith of the stem is relatively large, fills up the central portion, and

[1] The terms *vascular bundles* and *fibrovascular bundles* are often used interchangeably, even though strictly speaking the former should apply to bundles of conductive cells only and the latter to bundles that contain both conductive cells and thick-walled strengthening tissues.

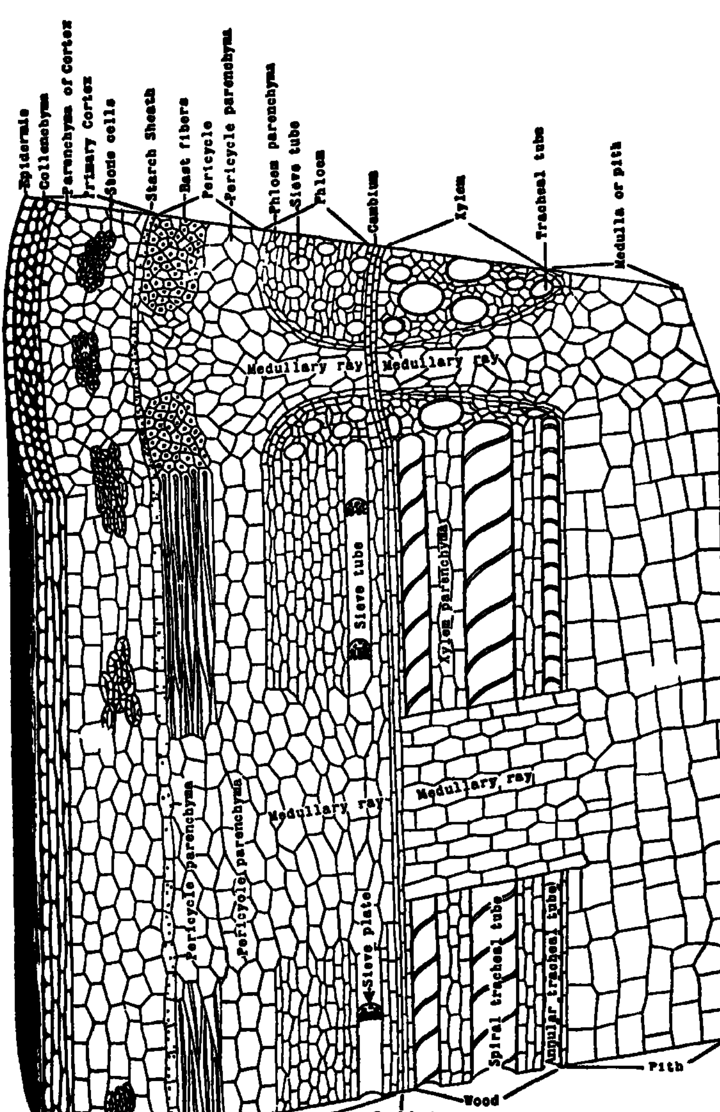


FIG. 52. Perspective view of a portion of a young dicotyledonous stem. Diagrammatic. (From Stevens' *Plant Anatomy*, P. Blakiston's Son & Co.)

extends out between the xylem regions to the cortex in the form of *medullary rays*, or *pith rays*.

Details of the Xylem.—To understand the process of raising the soil water from the ground to the top of a tree one needs to examine closely the system through which it is to travel. The xylem of most plants is composed of cells of several kinds. In the sunflower there are mainly two. (1) *Tracheids*, which are long, slender, pointed cells

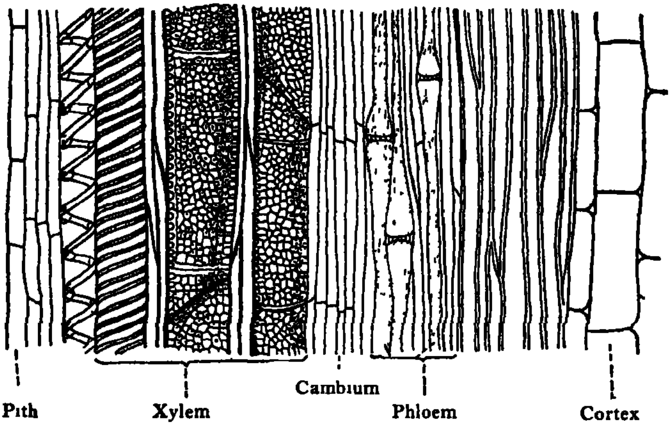


FIG. 53. Longitudinal section of a fibrovascular bundle of a sunflower stem Somewhat diagrammatic. (From Mottier's *Textbook of Botany*, P. Blakiston's Son & Co)

with walls that have thickened ridges in the form of rings or spirals. Their protoplasm disintegrates with maturity. They aid in the transport of sap up the stem. (2) *Vessel segments* that are generally larger in diameter than the tracheids. Their walls are likewise sculptured with thickenings of various designs. They, too, lose their protoplasmic contents, and their end walls dissolve away, forming vessels which are continuous tubes that readily conduct water and dissolved substances up the stem.

In most woody dicotyledons and in many other plants two other kinds of cells are common in the xylem: (1) *Wood fibers*, that have thick walls and small cavities. Generally they have pointed ends that overlap the ends of the fibers above and below them. These thick-walled cells give mechanical strength but do not conduct water or food to any appreciable extent. They are interpreted to be modified tracheids.

(2) *Wood parenchyma.* The term parenchyma is applied to cells that are thin-walled and contain living protoplasm capable of carrying on

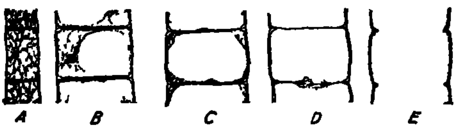


FIG. 54. Stages in the formation of xylem vessel, *E*, from vessel segment, *A*, by the dissolution of adjacent walls and loss of protoplasm, *B, C, D.* (From Eames & MacDaniels' *Introduction to Plant Anatomy,* McGraw-Hill Book Company, Inc.)

various activities, such as food manufacture and storage and even cell division under certain circumstances. Parenchyma is not confined to the xylem but is even more abundant elsewhere—in the pith, the cortex, and the leaves, filling up spaces between other tissues.

While both tracheids and vessels are found in the sunflower and in most other flowering plants, unmodified tracheids are absent from

FIG. 55. Cross-section of a young cedar tree showing heart-wood and sap-wood.

some, such as the willow, and vessels are absent from the pine and other cone-bearing trees.

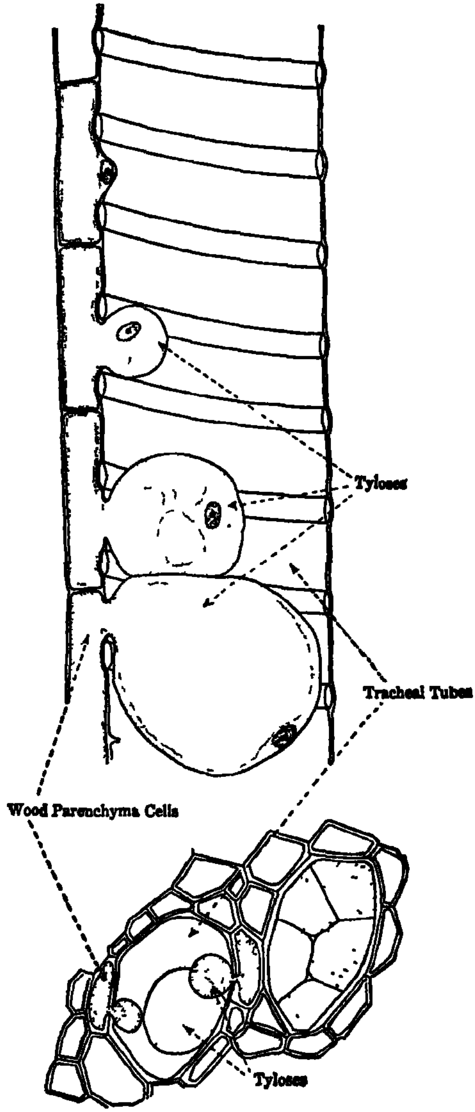


FIG. 56. Longitudinal and cross-sections of a xylem vessel of black locust, showing tyloses protruding into it from adjacent wood-parenchyma cells. (Reprinted by permission from *Textbook of General Botany*, Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc.)

Most trees have, just inside the bark, a layer of light-colored *sap-wood* surrounding a central region of dark-colored *heart-wood*. The sap-wood is younger, contains living cells, and conducts soil water up

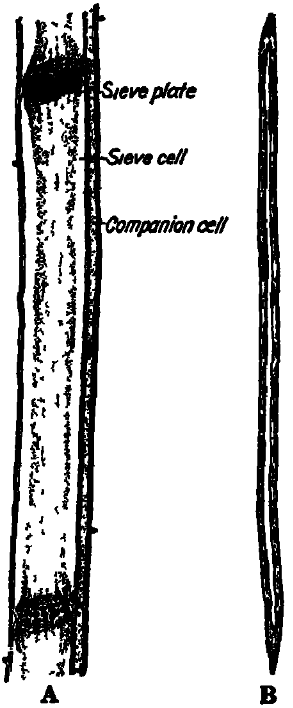


FIG 57 Cells from the phloem of squash A, sieve tube and companion cell, B, bast fiber (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company)

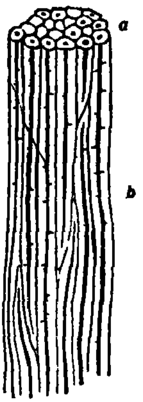


FIG 58 Group of bast fibers from phloem region (From Bergen and Davis' *Principles of Botany*, Ginn & Co After Tschirch)

the tree. The heart-wood is older and no longer functions in the ascent of sap. In some kinds of trees the change from sap-wood to heart-wood is preceded by the formation of *tyloses*, which are bladder-like extensions from the wood parenchyma that protrude into the cavities of the vessels and thus close them. This is followed by the death of all cells previously living in that portion of the xylem.

Details of the Phloem.—The phloem region is much smaller than the xylem, and the manufactured food that it carries is much more concentrated than the sap passing up the xylem. Three kinds of cells are commonly present: (1) *bast fibers,* (2) *sieve tubes,* and (3) *com-*

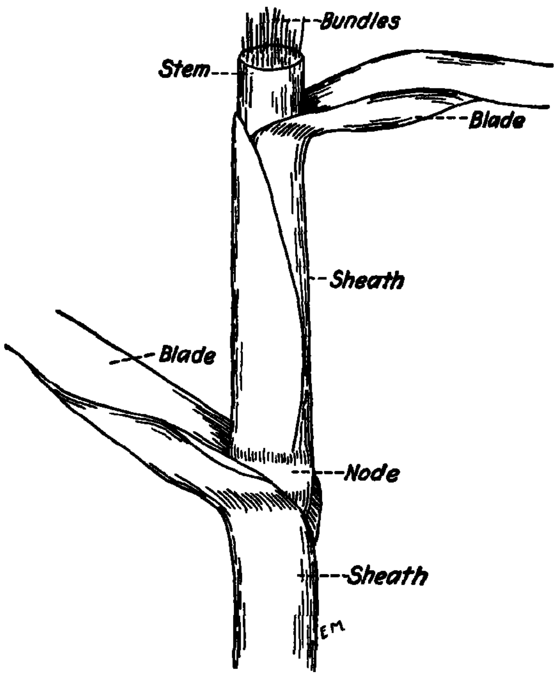


FIG. 59. Portion of corn stem, showing fibrovascular bundles protruding from broken end.

panion cells. There are also a few parenchyma cells. The principal function of the sieve tubes is to conduct manufactured food through the stem, chiefly toward the root. They lose their nuclei soon after their formation, but the cytoplasm remains and functions for some time. It has been suggested that the nuclei of adjacent companion cells or parenchyma cells aid the cytoplasm of the sieve tubes in some way, perhaps influencing the activities of these cells.

Where one sieve tube joins another end to end, the end walls are perforated and are called *sieve plates.* This is the most common con-

dition in flowering plants although some have sieve plates in the side walls. The companion cells, with much cytoplasm and large nuclei, are interesting in appearance, but their function is not certainly known. They are absent from the sunflower and some other species.

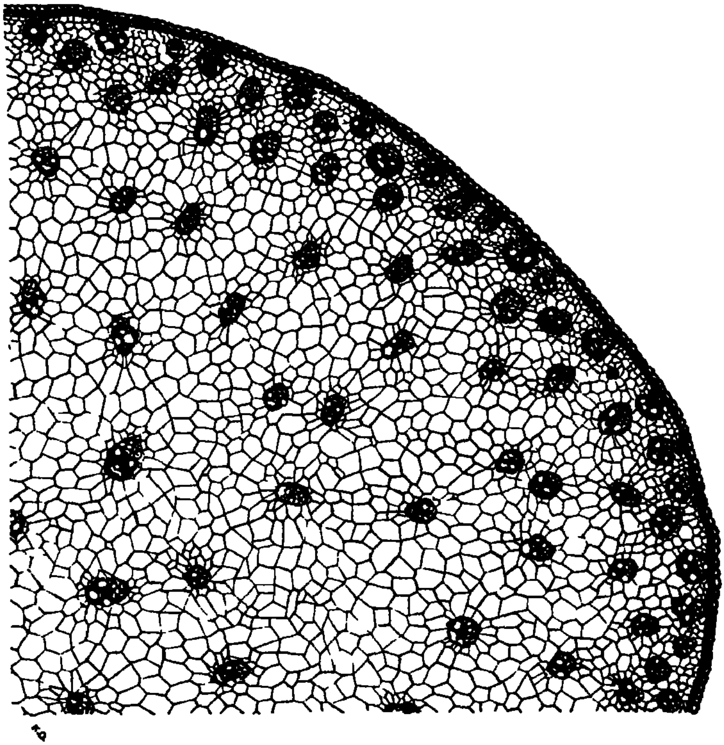


FIG 60. Cross-section of corn stem showing the distribution of fibrovascular bundles in a typical monocotyledon.

The Fibrovascular System as a Whole.—Structures such as these are meaningless until their purpose is known, when they take on a new significance. The xylem region serves to conduct the water and minerals from the soil up to the leaves, where they are needed in food manufacture, and to restore the water lost by evaporation. The phloem carries the manufactured food down from the leaves to the roots, some being diverted along the way to nourish the stem.

The fibrovascular system as a whole should be thought of as a collection of tubes, fibers, and other cells running lengthwise from root tips through roots, trunks, and branches, and out into the leaves, where they form the veins. It not only conducts water and food but also serves to give strength and rigidity. In a tree, for example, the phloem makes up the greater part of the bark, and the xylem makes up the

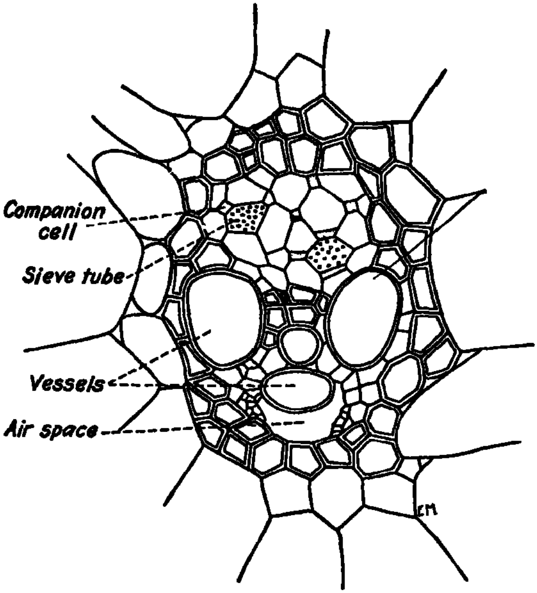


FIG. 61. Cross-section of a fibrovascular bundle of a corn stem.

wood. The cambium layer lies between. The fibrovascular system, then, constitutes the greater part of the body of a plant.

Dicotyledonous versus Monocotyledonous Stems.—The stem structure just described for the sunflower and some other plants is representative of the great group of dicotyledons. The stems of monocotyledons, represented by the lilies, corn, sugar-cane, and grasses, have a very different arrangement of fibrovascular bundles. Instead of being arranged in a hollow cylinder with cortex outside and pith inside, the bundles of corn, sugar-cane, and others with solid stems are scattered, the space between them being filled with parenchyma. There is no clear-cut distinction between cortex and pith, nor are the layers of

endodermis and pericycle sharply differentiated. The bundles are more numerous toward the periphery, and farther apart toward the center. The phloem portion of each bundle is toward the outside and the

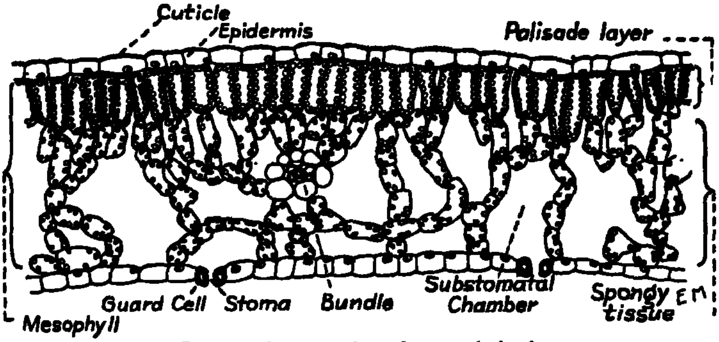


FIG. 62. Cross-section of an apple leaf.

xylem portion toward the center. Between the two there is no cambium layer, which is characteristic of *closed* bundles in contrast with the *open* bundles of most dicotyledons, in which there is a cambium layer.

In the great majority of the monocotyledons the bundles are very numerous and throughout the life of the plant they furnish an abun-

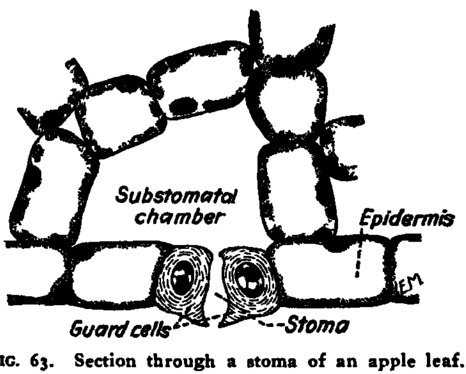


FIG. 63. Section through a stoma of an apple leaf.

dance of water to the dense foliage. As the plants grow older the lower leaves tend to die, and in large perennial species such as some palm trees only a dense cluster of leaves at the top remains alive and green.

In herbaceous species the cells of the epidermis and the tissues just beneath it are thick-walled. This hard, strong outer layer rather than a woody interior, such as is found in dicotyledons, gives rigidity to the stem, even though the inner portion is soft or even hollow, as in wheat and oats.

Leaf Structure.—The internal structure of a leaf of an apple or other plant can best be studied in vertical, or cross, section. In a manufacturing establishment we would expect to find a factory or group of factories with lines of transport entering from the outside. A leaf shows all these things.

On the upper surface there is a single layer of cells, the *upper epidermis*. The outer walls of the epidermal cells are considerably thickened by a smooth, waterproof layer, or *cuticle*. In some plants there is a considerable development of *epidermal hairs*. Just below the epidermis is the *palisade layer* of elongated cells set vertically close together, their cytoplasm densely filled with chloroplasts. In this position they receive light from the sun to the best advantage. Just below the palisade cells is a *spongy* layer, so called because of the abundance of large air spaces between the cells. The palisade layer and spongy layer together make up the *mesophyll*. It carries on most of the food manufacture. Through this mesophyll run the veins of the leaf, fibrovascular bundles in which the xylem is much more conspicuous than the phloem. Lastly, there is the *lower epidermis*, that has a cuticle much thinner than that on the upper epidermis and usually with more epidermal hairs.

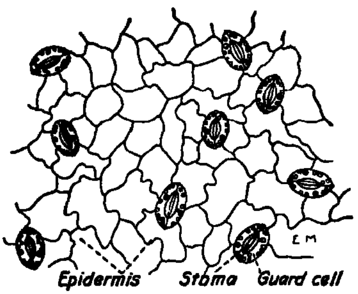


FIG. 64. Surface view of epidermis from geranium leaf, showing numerous stomata.

It is chiefly through the lower epidermis that provision is made for the entrance of air or, more strictly speaking, the exchange of gases between the air and the intercellular spaces of the leaves. Here may be found very numerous, tiny openings or *stomata*, sometimes improperly called "breathing pores." Each stoma is bounded by two *guard cells*, which when turgid hold the stoma open, but which when relaxed sag together and close it. The opening and the closing of the stomata are regulated to some extent by light and by other environ-

mental conditions, such as water supply. The intercellular spaces of the spongy layer permit free exchange of gases between the palisade cells and the stomatal openings.

Translocation of Water and Food

Now that a fair working knowledge of the transportation lines within the plant has been obtained, the processes of moving food materials and foods from place to place where needed will be taken up.

Path of the Soil Water.—Water in the soil, coming in contact with root-hairs, enters them, diffuses through the cells of the cortex, and passes on into the xylem vessels. Through these vessels it rises to the leaves, which it enters by way of the veins. There a portion is used in the manufacture of sugar and starch. Most of it, however, is lost by evaporation through the stomata, which must be open to admit carbon dioxide and oxygen. This loss of water vapor from the leaves is known as *transpiration*.

If during a warm day the air takes up considerable moisture, it may reach the saturation point the following night when the temperature is lower. Under these circumstances moisture will evaporate from the leaves less rapidly, and the pressure of sap from below may force water out in the liquid state through wide-open *water pores*, or *hydathodes*, which are found in many plants in the ends of the veins at the margins of the leaves. Some water probably passes out through the hydathodes at all times when the roots are well supplied, but while it is unnoticeable on a warm, dry day because of evaporation, it may accumulate in droplets on the leaves during a cool night. These droplets make up a portion of the moisture found on grass in the early morning and commonly called dew; but it should be understood that their origin is quite different from that of dew, which is water deposited from the air when it is supersaturated.

Intake of Water and Solutes.—The method by which root-hairs absorb soil water, with its dissolved minerals, is fairly well understood. It was explained in the discussion of osmosis earlier in this chapter. It must not be supposed that the mineral matter is carried in by the flow of water. The plasma membrane of the root-hairs being osmotic, each substance enters independently of the others.

Water and food materials pass readily through the cortex from the epidermis to the fibrovascular system by diffusion from cell to cell. There is no evidence that the cortex presents a serious barrier, and

plants have never evolved roots in which this layer has been eliminated or even reduced to a minimum thickness. It should be understood that water and dissolved salts do not have to pass through the phloem to reach the xylem vessels, *for in roots so young as those that bear root-hairs*, the xylem extends between the phloem bundles nearly to the cortex. Also, some water may reach the xylem by passing below the young phloem.

The Ascent of Sap.—Few problems in botany have proved more difficult of solution than the explanation of the forces that carry sap up to the leaves of a tall tree. There is reason to suppose that the mechanism for doing this is well perfected, for trees seem not to be limited in their height by difficulties in getting water to the top.

Explanations That Have Been Offered.—Based on extensive investigations in plant anatomy and on an understanding of certain laws of physics, a number of workers have proposed theories to account, in part at least, for the ascent of sap.

1. **Root Pressure** seems to be one important factor. The soil water, entering the root-hairs and passing on through the cortex by osmosis, tends to push up the stem ahead of it the water already in the xylem vessels. Recent experiments, using more refined technique than the earlier ones, have shown that tomato roots attached to manometers exert a pressure of the solution passing through them sufficient to carry it to the tops of ordinary trees, which far exceeds that calculated from earlier experiments in which the stumps of plants cut off above the ground were tested.

2. **Capillarity in the xylem vessels** has been offered as an explanation. If the end of a glass tube of very small diameter is set vertically in a dish of water, the water will rise in the tube a short distance above that in the dish. The narrower the bore of the capillary tube the higher the column of water will rise in it. The expected height to which it will rise can be calculated mathematically, but under perfect conditions it would, at best, carry the sap up only a few feet. *However, perfect conditions for the action of capillarity do not exist* in the xylem of a plant. Capillarity, as illustrated by water rising in a narrow tube, may be regarded as a result of forces acting at the surface of the liquid, causing it to adhere to the wall of the enclosing tube and move along it. As the xylem vessels are entirely filled with liquid, there is no such top surface to the columns within them. In a capillary tube entirely filled with liquid and closed at the top, there is no reason to expect a tendency to flow upward any more than down-

ward Hence, capillary action seems to be of no importance in carrying water up through the xylem vessels.

3 **Evaporation, imbibition, and cohesion.** The third explanation can best be understood by starting the study at the leaves and progressing downward. At their upper ends in the leaves the xylem vessels abut against cells of the mesophyll These cells are partly exposed to the air in the intercellular spaces of the spongy tissue. Water evaporates from the exposed walls of these cells into the spaces and escapes through the stomata This process tends to concentrate the solute in the cells of the mesophyll and to dry the exposed walls. As a result water moves by osmosis from the vessels into the mesophyll cells, and the walls are kept supplied with water from their protoplasts by imbibition. It might be expected that this withdrawal of water from the vessels would leave an empty space at the top of them, but such is not the case. The particles of water cohere with great tenacity, and as fast as some water passes into the mesophyll cells more follows it closely, leaving no space It has been shown, to the surprise of many people, that a closed column of water in a narrow tube has remarkable tensile strength. A great force is required to pull it apart or to make a break in it. Therefore, instead of the vessels' being emptied at the top, they remain filled by drawing on the supply below, the water being literally pulled up the stem.

This process must not be confused with the action of a "suction" pump. In such a pump the piston tends to create a partial vacuum above the water column, and atmospheric pressure on the water below forces it upward If there is an air space above the water column it makes no difference The pressure is from below In the plant there must be no vacuum or air space in the columns. They must be continuous, with no weak places

While some serious criticisms have been offered to this explanation of the rise of sap it is still regarded as one of great importance It is claimed that even though continuous water columns have considerable strength, the force necessary to break them is less than would be required to lift water to the height of a tall tree. This explanation of the ascent of sap has much merit, but alone it may not be sufficient

Summarizing the known facts, we conclude that the following forces work together to bring about the ascent of sap (1) Evaporation causes the water to be withdrawn from the mesophyll cells of the leaf (2) Imbibition and osmosis cause it to pass from the xylem vessels in the veins into and through the mesophyll cells. (3) The tensile strength

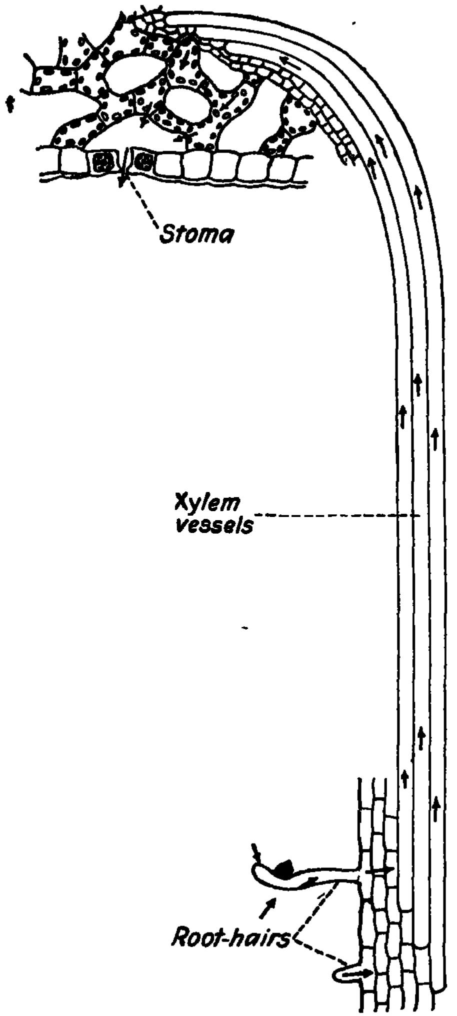


FIG. 65. Diagram illustrating the passage of water through a plant by the agency of evaporation from the cells in the leaf, which causes the passage of water through the cell walls by imbibition and a consequent pull on columns of water in the xylem vessels, aided by the intake of water by osmosis through the root-hairs.

of the water columns in the xylem vessels makes it possible for the forces in the leaf to draw the water up from the roots. (4) Imbibition and osmosis bring the water into the root-hairs, carry it through the cortex into the xylem vessels, and thus constantly supply the transpiration stream, and materially aid in its rise.

Whatever the forces may be that carry the sap up the stems of plants they seem to be ample for the purpose, for we see no evidence

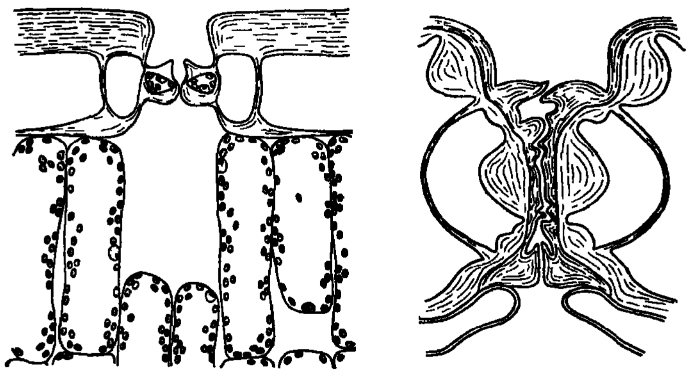


FIG. 66. Specialized stomata that reduce evaporation. Left, stoma of carnation sunken below the surface. Right, stoma of Nipa palm, with slender tortuous passage. (Modified from Bobisut)

that difficulty in getting water up to the leaves is a factor that limits the height of trees.

The preceding explanations are applicable to the more or less continuous rise of sap in plants during the growing season, when leaves are present and giving off water vapor. There is an old belief that "the sap goes down" in the autumn after the leaves are shed from the trees. For such a belief there is no scientific foundation. During the period when trees and shrubs are leafless there is comparatively little movement of water in any direction, and under normal conditions the wood does not become dry. Some trees and vines, such as maple, birch, and grape, if wounded in the spring, will "bleed" or discharge sap through the break in the bark. This sap appears to be under considerable pressure and flows toward the wound from above as well as from below it, i.e., some of it goes up and some comes down. However, it will never be lost to an extent that will leave the wood dry.

Transpiration.—The loss of water from plants in the form of vapor is much greater than is commonly supposed. The amount varies with the species of plant and with conditions, but a large sunflower plant under some conditions will transpire a gallon of water a day, and the daily transpiration of a corn field may reach fifty tons, or 397 barrels, to the acre. Some species of plants transpire much more freely than others. In some xerophytes very effective devices have been evolved that reduce transpiration without entirely excluding carbon dioxide. In many such plants the stomata are sunk below the surface so that the humid air issuing from them will not be quickly carried away but will retard the outward diffusion of water vapor. In the Nipa palm the stomatal openings are deep, narrow, and crooked, making the escape of water very slow. In *Pilea elegans,* which has stomata in the upper epidermis, a mesophyll cell at the bottom of the substomatal chamber projects upward and forms a plug or tylose. When the leaf is slightly wilted the guard cells fall and rest against this plug, and the escape of water is prevented. In the leaves of oleander there are cavities with narrow mouths communicating with the surface. The stomata are in the epidermal linings of these cavities. In the sand-reed and some other xerophytic grasses the stomata are in grooves. When the leaves wilt from lack of water they roll up, closing these grooves and confining the water vapor. In cacti the leaves have been reduced to hard spines and the stems, with fewer stomata, function as leaves. Thick, hairy coatings on the surfaces of leaves are fairly common.

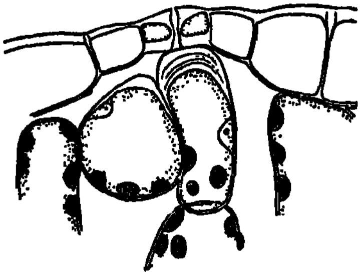


FIG. 67. Specialized stoma of *Pilea elegans.* When the leaf wilts, the guard cells and stoma settle against a special cell which closes the opening. (Redrawn from Haberlandt.)

Aside from structural modifications found in different plant species, there are a number of environmental conditions that affect transpiration. It is increased by light, elevation of temperature, lowering of humidity, air currents, and water supply in the soil. As would be expected from these facts, it is much greater in the daytime than during the night.

Why do plants transpire? Does it serve a useful purpose or is it a misfortune to the plant? The older idea was that the plant had to

collect a great volume of dilute soil water and evaporate it to obtain the necessary mineral food, but this idea has been abandoned. Land plants have to have open stomata to admit carbon dioxide. The transpiration of water through these stomata is unavoidable and will be harmful unless a supply of water is brought up from below by the transpiration stream to replace the loss. One other benefit is obtained from this transpiration stream. It carries a large proportion of the solutes up to the leaves. Minerals in solution enter the roots by osmosis, regardless of the inflow of water, but having entered the xylem vessels they cannot rise by osmosis, for there are no membranes across these tubes and the concentration in them is fairly even. Rise by diffusion alone would be extremely slow. Here the rise of sap, made necessary by transpiration, serves a useful purpose in the transport of food materials.

Transport of Manufactured Food

Foods are extensively manufactured in the leaves. They are needed for use elsewhere—everywhere in the plant. How are they transported? *In part this is known; in part it is puzzling.*

What Are Manufactured Foods?—To comprehend the methods of food transfer something should be known concerning the nature of the foods. In commercial enterprises different methods of shipment are used for different commodities, and so it is with the plant.

There are many different compounds produced by the plant. Two of the most important groups will be mentioned here, the sugars and the proteins. The sugars are soluble in water and *dialysable,* i.e., capable of passing through membranes osmotically. Many proteins, on the other hand, are insoluble in water and form colloidal suspensions that will not pass through the plasma membranes.

Transport of Sugars.—In some parts of the plant sugars are being formed. In other parts they are being used. We can conceive of the formation of a concentration *gradient* between these two points, i.e., a region in which the cells progressively contain less and less sugar. Under these circumstances diffusion and osmosis would aid in carrying the sugar from the place of supply to the place of demand.

Transport of Proteins.—Proteins, being colloidal, cannot be carried by simple diffusion and osmosis, and the processes by which they pass from cell to cell are not clear. There are instances in which they are broken down to simpler dialysable compounds, pass through the

membranes, and are then changed back to proteins. Whether or not this is of common occurrence in plant tissues is yet to be determined.

Transport through the Phloem Region.—It is quite generally agreed that the sieve tubes of the phloem are instrumental in very extensive translocation of sugars and proteins. They appear to carry food from the leaves all the way to the roots, leaving some which serves to nourish the body of the plant all along the line. The sieve tubes contain living protoplasts, and a circulation of the cytoplasm containing food has been seen in them. Through the sieve plates that form the end walls separating adjacent cells there are numerous holes. However, it is doubtful if solid particles of food pass through these holes. Doubtless sugars can readily diffuse from one sieve tube to the next, but a complete explanation of the passage of proteins has not been found.

One thing is certain. The manufactured food does not pass down the phloem by simple gravity. Indeed, under some conditions it is carried upward rather than downward. When such material passes into potato tubers, which are the tips of underground stems, or into fruits, which form the tips of branches, it is moving away from the root rather than toward it, and to supply some flowers and fruits it may actually rise against gravity. There is much evidence in support of the conclusion that foods move through the phloem in either direction as the needs of the plant require. The tendency for a manufactured food to pass downward through the phloem has here been emphasized, but it should be realized that it is transported in any direction through the plant and through tissues other than the phloem from regions where it is of relatively high concentration to regions where it is less concentrated.

Lateral Transport.—While most attention is given to the transport of water and foods up and down the stem, it should be realized that the living cells of the wood, and even the pith, must receive food from the phloem, and the cortex and the phloem have to receive water from the xylem. This lateral movement seems to take place, in part at least, by osmosis through the radial rays of parenchyma cells, the pith rays, and the vascular rays lying between the fibrovascular bundles. (See page 139.) During the dormant season some carbohydrates—sugar and starch—are stored in these rays, and supply food for the renewal of growth the next season.

In this chapter osmosis has been extensively used as an explanation of translocation, and undoubtedly it plays a major role; but it must be admitted that the osmotic membranes of living cells behave somewhat

differently at times from what we might have expected from our knowledge of physics. This may be explained by our limited knowledge of the physics and chemistry of living protoplasm.

Review Questions

1. Name the principal regions of a plant where food materials are received from the outside.
2. Name the food materials received in each region.
3. Explain the diffusion of gases in a room where there are no air currents.
4. Give an example of diffusion of liquids.
5. Give an example of diffusion of water.
6. Which is the more rapid, diffusion of gases or diffusion of liquids?
7. What is meant by the terms solvent and solute?
8. Give a definition of osmosis.
9. What is the difference between a permeable and a semi-permeable membrane?
10. In an osmosis experiment a sac made of a permeable membrane is suspended in a jar. The sac contains 90% water and 10% table salt. The jar outside the sac contains 50% water and 50% sugar. What will pass through the membrane, and in what direction will each pass?
11. What are colloids?
12. Why do colloids not pass through a membrane by osmosis?
13. Inside a sac made of a permeable membrane there is pure water. Outside it there is a colloidal suspension consisting of 5% gelatin particles and 95% water. In what direction through the membrane will each substance move and why?
14. What is meant by imbibition? Give an example.
15. Through what parts of a plant does water pass by imbibition?
16. Through what parts of a plant does water pass by osmosis?
17. Trace the course of water from the soil through the plant to the air outside the leaf.
18. Under any conditions could a solute pass into a root-hair without water passing in at the same time?
19. What is meant by a "gradient" for the continuous passage of sugar through a plant tissue?
20. What forces remove water from the leaves?
21. What is meant by root pressure?
22. What forces bring it about?
23. How can water be withdrawn from a cell?
24. Why do we not regard capillarity as significant in carrying water up the xylem vessels?
25. Explain what we know about the forces that cause sap to flow up a stem.
26. Why would air bubbles in a xylem vessel hinder the flow of sap?

27. Explain how the transpiration stream differs from the rise of water in a "suction pump": (1) as to the height to which it will rise, (2) as to the force that causes it to rise.
28. Why do plants transpire?
29. What conditions increase transpiration?
30. In what two ways is a plant benefited by the transpiration stream?
31. In what respect is transpiration a harmful process to a plant?
32. Describe the arrangement of tissues as seen in a dicotyledonous stem?
33. How does a monocotyledonous stem differ in this respect?
34. Name the kinds of cells found in the phloem.
35. Name the kinds in the xylem.
36. How does the arrangement of phloem and xylem in a very young root differ from that in a very young stem?
37. How does the structure of a very young root differ from that of an older root?
38. Give two ways of distinguishing roots from stems.
39. In the stem of a dicotyledonous tree, state which of the following are in the bark and which in the wood: (1) xylem, (2) cortex, (3) pith, (4) sieve tubes, (5) medullary rays, (6) epidermis, (7) pericycle, (8) companion cells, (9) cambium layer, (10) phloem.
40. How does the material that rises through the xylem vessels differ from that which descends through the sieve tubes: (1) as to volume? (2) as to composition?
41. Of what use to a tree is the heart-wood?
42. Give the functions of: (1) sieve tubes, (2) lenticels, (3) sap-wood, (4) bast fibers, (5) corky layer.
43. Describe the structure of a leaf as seen in cross-section.
44. Give the functions of each part of a leaf.
45. On which side of the leaf are most of the stomata, as a rule?
46. What factors cause the stomata to open and close?
47. How does carbon dioxide enter the cells of the leaf?
48. What are water pores? Their technical name? Their function?
49. How does girdling kill a tree?
50. Explain how sugar, for example, passes through tissues other than sieve tubes.
51. What is the function of the cuticle?
52. Define: (1) mesophyll, (2) stele, (3) guard cell, (4) petiole, (5) spongy tissue, (6) endodermis, (7) parenchyma, (8) herbaceous plant, (9) node, (10) sieve plate.

CHAPTER VIII

FOOD MANUFACTURE IN PLANTS

Of all living things plants have the greatest powers of food manufacture. They bring about a great variety of chemical changes, some of which cannot be duplicated by animals or by man. The term *metabolism* is applied to any chemical change brought about by a plant or an animal in relation to its food. If the change results in complex compounds being made from simpler ones it is called ***anabolism***. A good example is the making of glucose from carbon dioxide and water. Anabolism requires a supply of energy for its accomplishment. Light is used in the example just given, and the glucose thus contains ***potential*** *chemical energy* that can be released when needed. If the chemical change is in the nature of breaking down complex compounds into simpler ones, it is called *catabolism*. The best-known example is respiration, in which sugar is broken down into carbon dioxide and water, chemical energy being released in the process.

PHOTOSYNTHESIS

Light coming from the sun brings a great supply of energy to the earth. It might be expected that plants and animals through all the ages would have evolved many ways of utilizing this energy, but, as a matter of fact, there is only one that is of great importance. Even man with all his ingenuity has been baffled in his attempts to make a satisfactory engine driven by light. The one great method, the one which makes life on the earth a success, is ***photosynthesis***. It may be defined as the manufacture by green plants of sugars or other simple carbohydrates from carbon dioxide and water, using light as a source of energy. Oxygen is released as a by-product.

The Photosynthetic System.—It is evident that a process that is restricted almost exclusively to living green plants must be dependent upon a highly developed mechanism. This mechanism consists of those living protoplasts that possess chlorophyll, which is usually located in the

peripheral layer of the chloroplasts. For the use of these cells supplies of water, carbon dioxide, and light must be available.

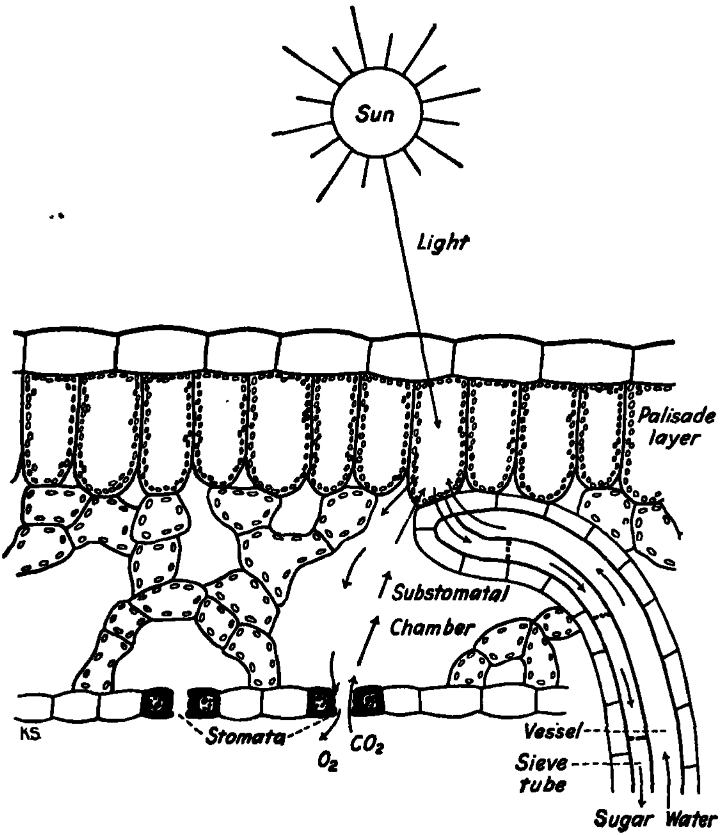


FIG. 68. Diagram illustrating the process of photosynthesis in a leaf—the intake of food materials, the action of light, and the exit of sugar and oxygen.

Probably under suitable conditions all cells that contain chloroplasts carry on photosynthesis. In the lower green plants these plastids are fairly evenly distributed among the cells, but in the higher plants there is more specialization. In the sunflower, for example, the cells of the cortex of the stem, the petioles, the spongy tissue, and even the guard cells of the stomata contain a few chloroplasts, but there are many more

in the cells of the palisade layer—the portion specialized for photosynthetic work. This layer is most favorably located in the upper half of the leaf with full exposure to light and with carbon dioxide and water close at hand in the spongy layer and the veins. Furthermore, the waste oxygen can here be eliminated through the stomata or used in respiration according to the needs of the plant, and the sugar formed can be carried away by the sieve tubes, leaving the palisade cells free for further work.

A remarkable part of the photosynthetic system is the device for obtaining the maximum absorption of carbon dioxide from the air without exposing the delicate cells of the mesophyll to mechanical injury or to excessive evaporation of moisture. The presence of stomata has long been known, and the efficiency of the action brought about by a combination of their number, size, and position was brought to attention early in the present century.

The number of stomata in different plants varies greatly. In most species the lower epidermis contains more than the upper. Indeed, a vast number of species, including the apple and peach, have none in the upper epidermis. A few plants, notably alfalfa and sweet clover, have more stomata above than below, and some hydrophytes with leaves that float on the water have all their stomata on the upper side. In the lower epidermis of most flowering plants the number is between 25,000 and 250,000 per square inch. For example, wheat has about 27,000, potato 100,000, cabbage 150,000, apple 200,000, and cucumber 275,000. These figures are, of course, only approximations, for the exact number varies somewhat with conditions.

Even though the number of stomata is very great, the proportion of the area of leaf surface that is given over to the aggregate of stomatal openings is relatively small, about one per cent being fairly common. This might seem to indicate that the absorption of carbon dioxide is greatly restricted, for practically none is taken through the epidermis between the stomata. Careful experiments have shown, however, (1) that diffusion through small pores is greater in proportion to their size than through large pores, (2) that the number of stomatal pores, considering their size, is about the optimum for the admission of carbon dioxide, and (3) that the amount of carbon dioxide that diffuses through the stomata and is absorbed by the cells of the mesophyll is about equal to that which would be absorbed by an equivalent area wholly uncovered by epidermis. This is indeed fortunate, for while the epidermis does

not decrease the intake of carbon dioxide to any great extent, it offers much protection against loss of water by evaporation.

The Photosynthetic Process.—Just how are carbon dioxide and water, two rather inert substances, made to combine into sugar? A vast amount of experimentation has been performed, and a considerable number of chemical theories have been evolved in the effort to answer

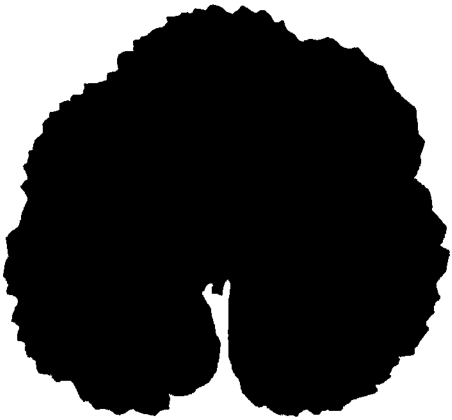


FIG. 69. Leaf of a geranium showing the importance of light in photosynthesis. The plant was kept in a dark room until its reserve starch had been used up or transported into the stem. Then the leaf was covered with tinfoil having an opening in the form of a letter S. After exposure to the direct sunshine for three hours, the iodine test showed starch only where the leaf had been lighted through the hole in the tinfoil.

this question, but the successive steps in the process are still a subject of controversy. There is some evidence that formaldehyde is an intermediate product, and this idea is embodied in more than one theory. Probably the first carbohydrate resulting from photosynthesis is dextrose or some other simple sugar. This, however, is quickly changed to starch in most plants. Water and carbon dioxide together contain oxygen in a larger proportion than is found in dextrose, and the excess oxygen is released as a by-product.

Even though the chemical steps of photosynthesis are not yet known, much of value has been learned. That starch is often the final product can easily be shown. If a plant, such as a potted geranium, is kept in darkness for a day or two it will have used up most of its reserve starch, as can be shown by applying to a leaf the iodine test for starch. A leaf

on such a plant can then be partly covered with tinfoil to keep a portion dark while the rest is exposed to the light. After the plant has stood in the direct sunlight for a few hours the leaf can be removed and given the iodine starch test. The presence of a blue color in the lighted portion but not in the covered portion indicates (1) that starch was formed where conditions were right for photosynthesis to take place, and (2) that without light photosynthesis cannot go on.

That oxygen is given off as a by-product is likewise easily shown. If some aquatic plants, such as *Elodea,* that naturally live submerged in water are placed in the sunlight, gas bubbles may be seen rising from the leaves and from the broken ends of the stems. These bubbles can easily be collected by means of a large glass funnel with a test tube filled with water inverted over its stem. Testing with a glowing splinter shows this gas to be oxygen.

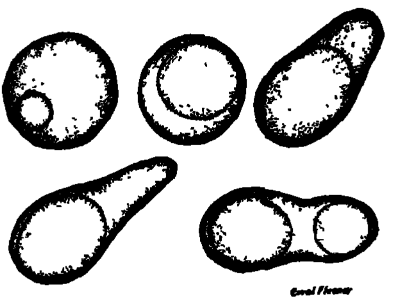


FIG. 70. Chloroplasts of *Elodea* leaf containing starch grains. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc.)

Conditions Favoring Photosynthesis.—Light as a necessary factor has already been mentioned. Just how the energy of light is transformed into the chemical energy in dextrose is another of the unsolved problems. Passing sunlight through a prism reveals it to be made up of the seven colors seen in a rainbow. Each color represents a certain range of wave length of light. It has been found that chlorophyll absorbs light of certain wave lengths more readily than others. For example, it absorbs the red, blue, and a portion of violet much more freely than the yellow and green. It has also been shown that portions of the red and blue furnish practically all the energy used in the photosynthetic work of higher plants. There is no question but that if light of certain wave lengths, as yellow and green, has not been absorbed by chlorophyll, it has not been used. Some of the absorbed light, however, is not used for this purpose. Therefore, there is not always a direct relation between the amount of light absorbed from different parts of the spectrum and its use in photosynthesis.

Chlorophyll does not occur alone but mixed with other pigments. These in the higher plants are xanthophyll and carotin. Some lower

plants, notably certain seaweeds, have supplementary red or blue pigments that enable them to carry on photosynthesis with light waves other than those utilized by chlorophyll.

The low percentage of carbon dioxide in the air seems to be a limiting factor in photosynthesis in regions where sunny days are the rule. A much higher percentage of this gas, up to one per cent or even more for some plants, is much nearer the optimum than is the 0.03 per cent generally found in the air. To utilize the existing amount of carbon dioxide a temperature of 98° to 100° F. is favorable, but if the carbon dioxide were more abundant a higher temperature would be better. The most brilliant sunlight is a little too strong for the utilization of 0.03 per cent of carbon dioxide, although it would not be too much for 0.1 to 1.0 per cent, but it is better than shade for the existing amount. Water also is necessary, but except in arid regions this is not ordinarily a limiting factor in photosynthesis. Lastly, the carbohydrates formed in the process must be transported from the cells or else they will slow down photosynthetic work.

Glucose is produced by photosynthesis in all cells that contain chlorophyll, very abundantly in the palisade cells of the leaves. From that region a portion is carried away at once by the sieve tubes and used elsewhere, but some is changed to starch and stored temporarily in the leaves. Later it is changed back into glucose and removed in that form, the sieve tubes being unsuited for the transportation of solid starch grains.

Respiration in Plants

In the whole realm of living things no process is more universal than respiration. In all animals and all plants, under all conditions while life remains, there is more or less respiration. The ability to respire should be included in the definition of life. What, then, is this process upon which life is so dependent?

Respiration versus Breathing.—Respiration is a chemical process in which oxygen unites with other elements or compounds, with the result that chemical energy is released for the use of the animal or plant body. The commonest products of respiration are carbon dioxide and water. Breathing, on the other hand, is the mechanical process of pumping air into the animal body so that it can be taken up and used in respiration. Plants respire but they have no way of breathing.

Energy Requirements.—It has long been known that energy takes various forms, and many processes are based on changes of energy from

one form into another. For example, an electric motor can change the energy of electricity into motion Many substances possess chemical energy, notably gasoline, alcohol, carbohydrates, and oils Such energy can be released for use by oxidizing these substances into such simple compounds as water and carbon dioxide, which have much less stored energy This oxidation, with its release of energy, can be accomplished by combustion, as in an engine or by respiration, which is the method used by animals and plants.

Plants, as well as animals, have much need for energy Energy is required for locomotion among some of the lower plants, for protoplasmic movement, and for nuclear and cell division. Most of all, it is needed for the building of protoplasm and cell walls from the simple food materials—carbon dioxide, water, and minerals Such complex substances as proteins, carbohydrates and oils have much more potential or stored energy than the same amount of the simple food materials Energy is required to build up these complex substances The energy for making sugars comes from light through photosynthesis, but the plant is unable to use light directly for the synthesis of proteins, nor can most plants use it for the synthesis of oils The energy for making proteins and most other complex materials comes through respiration, which releases it from the sugars and makes it available for other constructive work

From the foregoing it is obvious that an unusual amount of energy is needed when rapid growth is taking place, as in germinating seeds and expanding flowers Here, correspondingly, respiration is very rapid as measured by the amount of carbon dioxide released Oxidation of sugars and other foods, and possibly of the protoplasm itself, takes place and carbon dioxide is excreted as a waste product A part of the energy thus released is used for growth processes, and a part is changed from the potential energy or chemical energy of the stored food into heat, which escapes into the surrounding air, soil, or water and is lost as far as the plant is concerned

We thus see that the utilization of energy by green plants is in two steps (1) the accumulation of potential energy by photosynthesis, and (2) the release of this potential energy for the needs of the plant by respiration.

Respiration an Index of Activity.—We learn from observation that a running animal breathes rapidly and thus supplies oxygen for his rapid respiration and release of energy In plants the most active respiration is in connection with vigorous growth. Try the other extreme

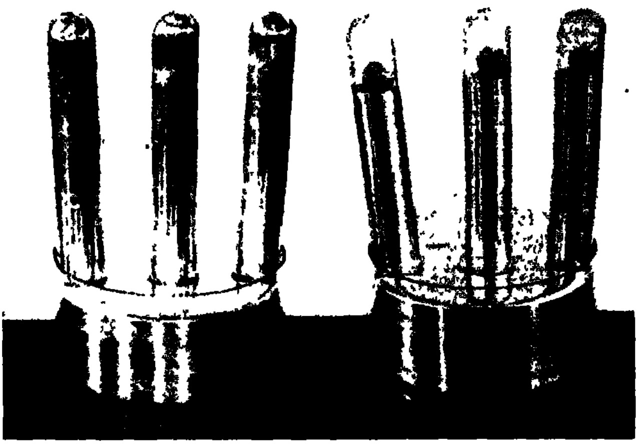
and name conditions where respiration is slowest. In dormant plants or parts—woody plants in winter, dormant bulbs, tubers, seeds, etc.—it is at the minimum. The release of minute quantities of carbon dioxide has been detected even in these dormant structures.

It has been emphasized that carbon dioxide is released in respiration. If this takes place during the daytime, some or all of it does not leave the plant but is absorbed by cells containing chlorophyll and is used for photosynthesis. The greater part of the carbon dioxide, all that forms during the night, escapes into the atmosphere and adds to the supply there.

Photosynthesis and Respiration Compared.—Respiration has been referred to as the reverse of photosynthesis. It is a valuable study in botany to determine in what respects this is true and in what respects the contrast fails. In photosynthesis water and carbon dioxide are used; in respiration they are given off. In photosynthesis oxygen is given off; in respiration it is used. In photosynthesis chemical energy is stored; in respiration it is released. Photosynthesis takes place in the daytime; respiration takes place not only at night but all the time. Only plants with chlorophyll carry on photosynthesis, but all plants and animals respire. The chemical steps in photosynthesis are not certainly known, but there is no reason to suppose that they are the exact reverse of those in respiration. From an economic standpoint both are of vital interest to man.

Anaerobic Respiration.—In ordinary, or *aerobic,* respiration free oxygen is used, generally from the air, but there is also an *intramolecular,* or *anaerobic,* respiration. In this exceptional form of respiration the atoms in molecules containing oxygen, for example sugar, are rearranged in such a way that energy is released and carbon dioxide is given off, and the remaining substance has a lower potential energy. If a living pea seed is soaked in water until it swells, it will start to germinate. In germination respiration becomes very active. If the seed is kept away from the oxygen of the air, intramolecular respiration will be set up within it. Such a seed inserted in an inverted tube of mercury will rise to the top, where there is no air. The next day, however, it will be surrounded by a considerable amount of gas that it has evolved. This gas can be absorbed by a bit of potassium hydroxide, showing it to be carbon dioxide. Some kinds of bacteria and yeasts likewise carry on anaerobic respiration and evolve carbon dioxide if air is excluded and they are given a supply of sugar and other suitable food.

It should be understood that oxygen is used in both kinds of respiration; the difference lies in its source. In aerobic respiration it is free or atmospheric oxygen; in anaerobic respiration it is in the form of oxygen compounds.



A B

FIG. 71. Demonstration of anaerobic respiration in pea seeds. In A a soaked pea seed has just been inserted into each of three inverted tubes filled with mercury and has risen to the top. In B the pea seeds, during an interval of 14 hours, have given off a considerable amount of carbon dioxide, which has replaced the mercury in the upper end of the tube.

When chemical energy is released we know some of the forms into which it is changed, but knowledge as to the details of the transformation is meager.

SYNTHESIS OF PROTEINS

All living things have the power of building proteins. It is thus that they make their own protoplasm, which is largely a mixture of proteins, and they often store away nitrogenous food supplies. While leaves participate in the synthesis of proteins, the process is more general throughout the plant than is photosynthesis.

There is a striking difference in the synthesis of proteins in plants and in animals. The raw materials from which plants make proteins are varied. They include water, simple nitrogenous compounds such as

nitrates and ammonia, sulfates and other mineral salts, and carbon compounds, of which sugars are the most important. In green plants some of the products of photosynthesis combine with water and minerals from the soil to form the proteins. Animals, on the other hand, cannot use such simple materials in the synthesis of their proteins but require a supply of proteins or other organic nitrogenous substances already made by other animals or plants. In the processes of animal digestion these materials are broken down, but not so far as to form ammonia or nitrates, and later the resulting products are reconstructed into the proteins of the animal body.

The steps by which proteins are made have been the subject of much study. There are thousands of different kinds of proteins, varying considerably in composition but all having large molecules of great complexity. All proteins contain carbon, hydrogen, oxygen, and nitrogen in various proportions and some contain sulfur, phosphorus, and other elements as well. A few simple proteins have been made synthetically in the laboratory. It is known that a source of energy such as that released by respiration is required. A few technical facts and theories of value have been deduced, but these are beyond the scope of this book.

Elimination of Waste

Plants in their nutrition do not take in as much useless material as do animals and have correspondingly less waste to eliminate. Even leaving out of consideration undigested material that has passed through the alimentary tract without ever having been incorporated into the body tissues, there is still urea, an important waste product of animals but not of plants. Aside from oxygen given off as a by-product of photosynthesis, the waste matter of plants is practically restricted to two kinds, carbon dioxide and useless minerals. Carbon dioxide must be looked upon as a waste product of respiration, even though it is later used by the plant in photosynthesis.

Carbon Dioxide Elimination.—Carbon dioxide is given off by all living cells, but we must keep in mind that the palisade cells and others carrying on active photosynthesis may use the carbon dioxide of respiration as fast as it is released. Under ordinary circumstances the carbon dioxide of respiration does not form gas bubbles within the cells but is dissolved in the cell sap and transported either through the cells or through the intercellular spaces to the surface of the plant, where it is given off through the stomata and, to a small extent, through the roots.

This is most easily detected in the night, when none of the carbon dioxide released is being used for photosynthesis. Germinating seeds in which respiration is active and which have no chlorophyll are especially favorable for studying this elimination.

Elimination of Mineral Matter.—Whether or not the roots of plants have any power of selection in the materials they absorb has been the subject of much investigation and speculation. In any event they do take up some minerals that are not used by the plant. Obviously these minerals would, in time, become a burden if there were no means of getting rid of them.

If the student will attempt to invent a method whereby a plant can eliminate such chemicals as calcium carbonate, calcium oxalate, and the various silicates, he will appreciate the difficulties. Plants have evolved one very satisfactory way. In the autumn when the leaves are burdened with minerals they are shed, and a new set is produced the next spring to take their place. This, then, is one of the several advantages gained by the shedding of leaves.

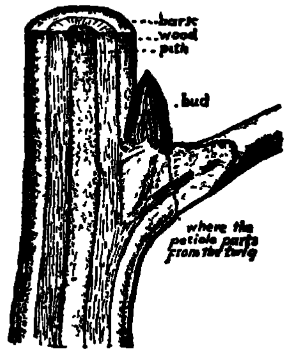


FIG. 72. Longitudinal section through a stem and the base of a petiole, showing the abscission layer by which the leaf is detached. (From Robbins' *Botany of Crop Plants*, P. Blakiston's Son & Co. After Longyear.)

A rather clever method is used by trees and shrubs for detaching their leaves. When conditions are right an *abscission layer* of cells forms across the petiole close to the stem. This is, in reality, a plate several cells in thickness. The walls of the cells in that portion of the layer farthest from the stem weaken so that they are easily broken by the wind, while the walls of those remaining on the tree become corky and protect the wound. This healed-over wound is called a *leaf scar*.

In *deciduous* trees and shrubs in northern latitudes the abscission layers form almost simultaneously in all the leaves, and the trees are left bare throughout the winter. In "evergreen" trees the leaves remain more than a year, and abscission occurs more or less continuously, removing the older leaves but never denuding the tree.

Nitrogen Metabolism in Plants.—All higher animals make extensive use of nitrogenous compounds, and when catabolic changes make these no longer useful they are eliminated in the form of urea. In

plants, however, the situation is quite different. They use only as much nitrogenous material as is required for growth and reproduction, and none is eliminated. Probably the lack of muscular activity in plants is, in part at least, responsible for the difference. In any event, the nitrogen economy in plants seems highly perfected.

Food Storage

Plants, like animals, have periods of abundance and periods of want. No photosynthesis takes place at night, and drought and cold

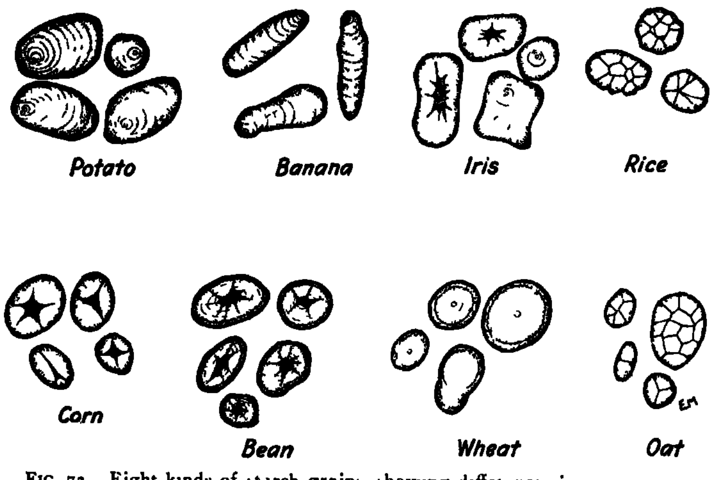


Fig. 73. Eight kinds of starch grains, showing differences in appearance.

cut down food manufacture. The new generation is helpless for a time to make its own food and must be provided with a temporary supply in the seed.

Kinds of Stored Food.—What constitutes a complete ration for plants? Aside from oxygen and water, which are generally available to the germinating seed and do not need to be stored, there must be carbonaceous food, nitrogenous food, and some mineral food materials. Only small quantities of the last named are required, and the other two are the ones most extensively laid away.

Starch is by far the most abundant storage product of plants. It is a very concentrated food, and when dry it is fairly safe from decomposition. It exists in the form of grains, often a large number

to the cell. These grains vary somewhat in appearance in different species of plants. They are insoluble in water and cannot be transported from cell to cell without being changed into sugar. The whole procedure of starch manufacture in the leaves and storage elsewhere in the plant makes an interesting picture. Photosynthesis forms glucose which is temporarily changed to starch, thus keeping down sugar concentration in the cell. During the night, when photosynthesis has ceased, the starch is changed to sugar and transported from the cell, some being used for growth and for other purposes. The excess is again changed to

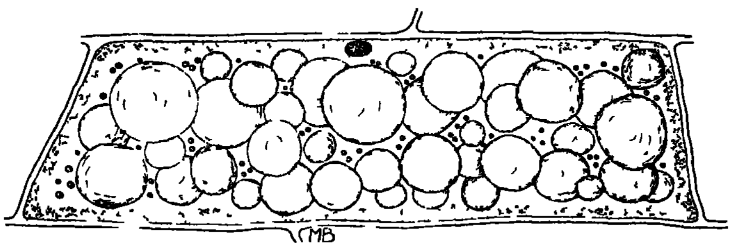


FIG. 74. Cell from endosperm of cocoanut showing many large oil drops and small protein grains

starch for storage purposes in tubers, fleshy roots, seeds, etc. In this storage process another kind of plastid is involved. These are the leucoplasts, which are colorless and, therefore, cannot carry on photosynthesis. They cannot make starch from carbon dioxide and water, but they can make it from sugar. If exposed to light they may change to chloroplasts. A few plants, notably the sugar-cane and sugar-beet, store their carbonaceous food as sugar.

Oil or fat is sometimes formed, and a portion may be stored, particularly in seeds. Corn, cotton, flax, peanuts, and the "castor bean" are good examples. Oil is usually stored in vacuoles or in globules in the cytoplasm but occasionally in special plastids or even in the cell wall.

The nitrogenous storage product is usually some kind of protein. The most familiar example is the gluten of wheat. There it is in the form of *aleurone,* which is also found in beans and many other seeds.

Some plants, for example "milkweeds," dandelions, lettuce, poppies, and the rubber plants, contain long, branched tubes that run throughout their tissues. These are *latex* tubes and they contain different ingredients, varying with the species. The most common of these are

gums, resins, starches, oils, proteins, alkaloids, and sugars. Latex is commonly regarded as storage material, although the correctness of this interpretation is not certain.

From the latex of various plants man has obtained a number of useful products. Opium comes from the latex of the poppy and yields the

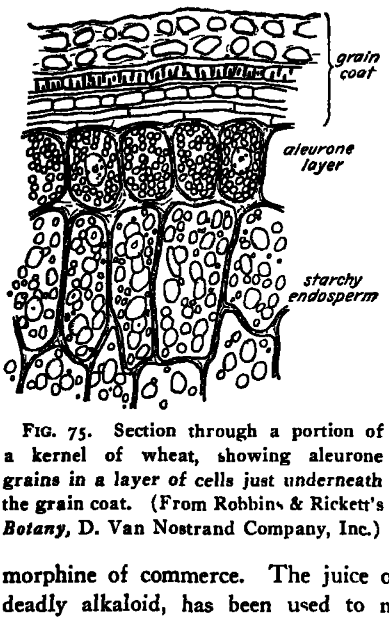


FIG. 75. Section through a portion of a kernel of wheat, showing aleurone grains in a layer of cells just underneath the grain coat. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

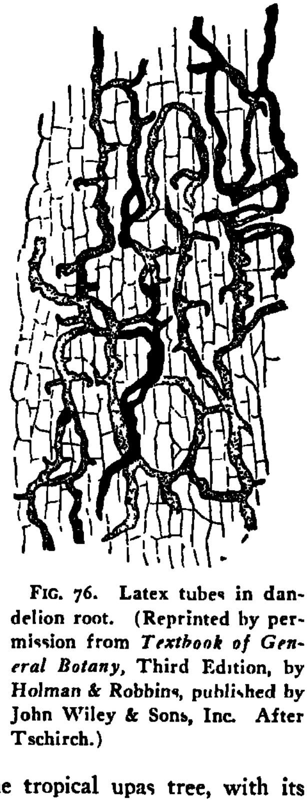


FIG. 76. Latex tubes in dandelion root. (Reprinted by permission from *Textbook of General Botany*, Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc. After Tschirch.)

morphine of commerce. The juice of the tropical upas tree, with its deadly alkaloid, has been used to make arrow heads poisonous. A nutritious beverage is made from the cow-tree of South America. Of great importance is the rubber of commerce, obtained from several species of rubber tree.

Regions for Food Storage.—Annual plants store very little food except in the seed. Each biennial and perennial stores it in its own way. In herbaceous plants some one organ is generally enlarged for

storage purposes—the roots in beets, carrots, parsnips, and sweet potatoes, tubers *in the potato, stems in* kohlrabi, *and leaves in* cabbage. In trees and shrubs no special organs are reserved for storage, the bark and the parenchyma of the sap wood being chiefly utilized.

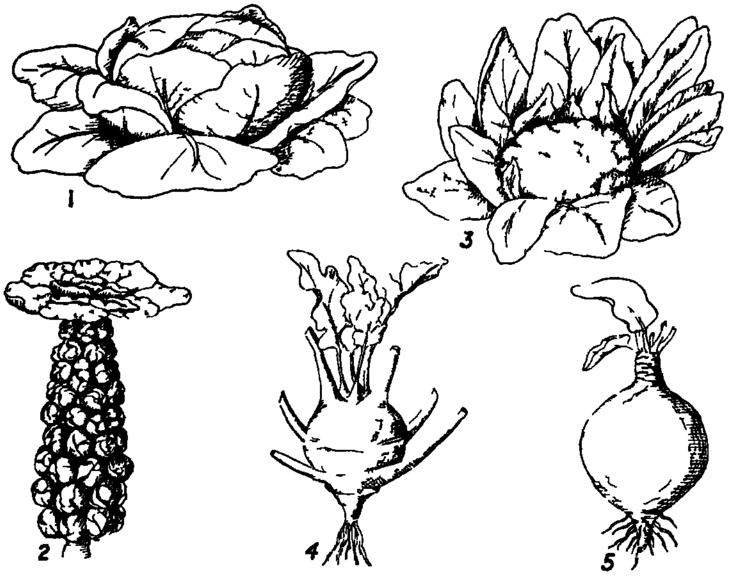


FIG 77 Food-storage organs 1, leaves of cabbage 2 buds of Brussels sprouts, 3, inflorescence of cauliflower, 4 stem of kohlrabi, 5 root of rutabaga All these plants belong to a single family—the Cruciferae (Redrawn after Gager)

Practically all higher plants store food in their seeds in sufficient amount and kind to nourish the young plant until it becomes independent.

REVIEW QUESTIONS

1 What is meant by metabolism?
2 What are the two divisions of metabolism?
3 In what two respects does anabolism differ from catabolism?
4. Give an example of each
5 What part of a plant is most active in food manufacture?
6. What are the chief kinds of food formed in a leaf?
7. Name an anabolic process that most plants can carry on but most animals cannot

8. In photosynthesis: (1) What raw materials are used? (2) What valuable product is formed? (3) What by-product is formed? (4) Is energy stored or released? (5) What is the source of energy?
9. What is the advantage of having the palisade layer near the upper surface of the leaf?
10. How does the palisade layer obtain for photosynthesis (1) water and (2) carbon dioxide?
11. What advantage is it to a plant to have a spongy layer with large intercellular spaces between the stomata and the palisade layer?
12. Which of the following plants carry on photosynthesis (1) pine, (2) willow, (3) onion, (4) mushrooms, (5) seaweeds, (6) molds?
13. Explain why some plants do and some plants do not carry on photosynthesis
14. What portions of the spectrum are most active in photosynthesis?
15. In what parts of a sunflower plant does photosynthesis take place?
16. Which of these is the most important for this purpose?
17. In the matter of photosynthesis what advantage do terrestrial plants have over submerged plants?
18. What becomes of the by-product oxygen?
19. What cell organs participate in photosynthesis?
20. *Name two chemical substances intermediate between the raw food* materials and starch
21. Explain how the excess starch is removed from leaves
22. State the conditions that favor photosynthesis
23. Why is energy needed for photosynthesis?
24. How could you prove that light is essential for photosynthesis?
25. How could you prove that carbon dioxide is essential for photosynthesis?
26. Does the presence of an epidermis cut down the amount of carbon dioxide available to the leaf? Explain
27. Why would it not be better for plants to have their stomata in the upper epidermis of the leaves close to the palisade layer?
28. Name a plant that has them so placed
29. What conditions are most favorable to photosynthesis as to (1) temperature, (2) light intensity, (3) percentage of carbon dioxide in the air?
30. Give the significance of photosynthesis to plants and to animals
31. Define respiration How does it differ from breathing?
32. How universal is respiration (1) as to kinds of plants and animals, (2) as to their state of activity or dormancy?
33. Of what value is respiration to plants and animals?
34. Under what conditions is respiration most rapid?
35. What becomes of the energy released in respiration?
36. How does anaerobic or intramolecular respiration differ from aerobic respiration?
37. Compare photosynthesis with respiration, pointing out all similarities and all differences
38. What materials enter into the formation of proteins?

39. What is the source of energy for the synthesis of proteins?
40. Explain the need of food storage by plants.
41. What are the chief kinds of food stored?
42. In what forms are each of the following stored: (1) carbohydrates, (2) oils, (3) proteins?
43. What parts of the plant are most used for food storage? Illustrate.
44. Give the functions of the following: (1) veins of the leaf, (2) stomata, (3) palisade cells, (4) petiole, and (5) epidermal hairs.
45. What kinds of waste material are eliminated by plants?
46. How is each eliminated?
47. Compare the elimination of waste nitrogen compounds in plants with that in animals.
48. Name two purposes served by the shedding of leaves.
49. What is the mechanism by which leaves are shed?
50. Define: (1) metabolism, (2) catabolism, (3) osmosis, (4) plasmolysis, and (5) anabolism.
51. Name five kinds of specialized leaves.

Part Four

THE GROWTH OF PLANTS

CHAPTER IX

ELONGATION OF ROOTS AND SHOOTS

To understand the growth of plants one must be able to answer at least five questions. (1) Do all cells participate equally in growth, or are there special growth regions? (2) How do the component cells, the units of life and structure, bring about growth of the entire plant? (3) Does growth take place uniformly in all directions? (4) What conditions favor the most rapid rate of growth? (5) Do plants, like animals, have growth-promoting substances such as hormones?

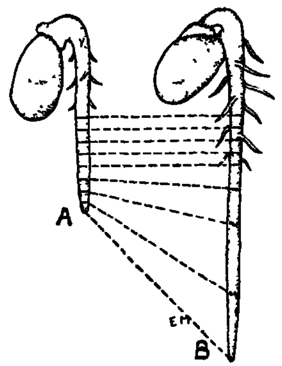


FIG. 78. Roots of squash marked to determine region of elongation. B was drawn 22 hours after A.

GROWTH REGIONS

We find in plants certain regions where growth *is taking place. In these regions* cells multiply by division, thus forming new ones, some of which continue to divide and remain small, while others enlarge, usually by elongation. Regions where new cells are forming are called meristematic, or embryonic. They are found in the tip of roots and stems, in the cambium layer, in young flower buds, and in a few other places, and are characterized by relatively small cells with dense cytoplasm, large nuclei, and absence of large central vacuoles.

ELONGATION OF ROOTS

There are two methods of determining the growth regions for elongation.

Experimental Study of Elongation.—If one has the terminal portion of a growing root exposed to view in a moist chamber and marks it with India ink at regular intervals of one-eighth inch from the tip

backward, he will discover in a day or two that the region of elongation is very limited. The mark at the extreme tip will have been carried forward by growth of the region between it and the next one back. There will have been considerable extension between this second mark and the third, and perhaps a little between the third and the fourth, but farther back the spaces will still be one-eighth inch apart. This experiment shows that all the growth is forward of the root-hairs.

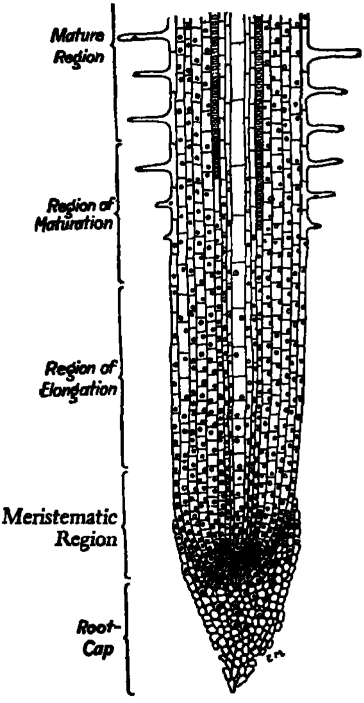


FIG. 79. Longitudinal section of onion root, showing the regions of development.

Internal Anatomy.—A microscopic study of a longitudinal section of a root tip is very instructive. One immediately notices a region just back of the extreme tip where new cells are forming by division. Stages in nuclear and cell division are frequent in this region but not elsewhere.

The meristematic cells of the root tip are relatively small and very compact in appearance, being densely crowded with protoplasm. The nucleus is large for the size of the cell, and the vacuoles are so small as to be quite unnoticeable. The walls are very thin. This appearance is characteristic of meristematic cells everywhere.

Forward of the meristematic region is the root-cap, the cells of which are being worn away by the passage of the root tip through the soil. However, new cells from the meristematic region keep replacing those lost from the root-cap so that it persists as a permanent structure.

On examining the root from the meristematic region toward the older portion it is seen that the cells have greatly elongated. Indeed, they are practically as long a quarter of an inch from the tip as they are farther back, a fact which corresponds with the information gained by marking the roots. This, then, is the *region of elongation.* The

cells during their growth have not perceptibly increased the amount of protoplasm. The original quantity was sufficient. What was needed was longer cells to advance the root into the soil. This elongation was gained in the most economical way—by the addition of water to the vacuoles so that they enlarged and coalesced to form a central vacuole occupying a large portion of the protoplast.

In the region of elongation, as in the meristematic region, the cell walls are thin and show no specialization. A little farther back from the tip, however, they begin to change into sieve tubes, cambium layer, xylem vessels, etc. The bundles produced by the meristem are called *primary* bundles to distinguish them from the *secondary* phloem and xylem that are added later by the cambium layer. The primary fibrovascular bundles grow in length by additions to their lower ends. As new cells are formed in the meristem, they elongate and then differentiate into the cells of the fibrovascular system and other parts of the young roots. Thus as the roots grow in length, the primary bundles elongate correspondingly.

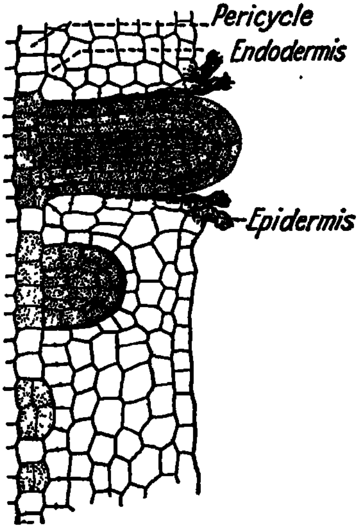


FIG. 80. Longitudinal section of a portion of a root, showing four stages in the origin of a branch root. (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company, Inc.)

The portion where the cells are maturing to fill their ultimate destiny is called the *region of maturation*. It grades imperceptibly into the *mature region* where the phloem and xylem are well established. The root-hairs are restricted to the region of maturation and the lower, younger portion of the mature region. New ones are sent out as the root grows, and the older ones an inch or so back shrivel and disappear.

The advantage to the plant of having the root-hairs restricted to that portion of the root is easily seen. If they were nearer the tip they would be stripped off as the root tip pushes into the soil. If they remained on the older portion of the root, where growth in diameter has

taken place, soil water entering them would have greater difficulty in passing from them to the xylem vessels.

Formation of Branch Roots.—As previously stated, roots have no nodes. At certain points, however, cells of the *pericycle,* which is the outer cell layer of the stele, begin to divide and start new meristematic regions. These newly formed growing points push out through the cortex and epidermis, crushing cells as they advance, until they break through the surface and enter the soil as branch roots. When roots are broken off or otherwise injured, new roots may grow from the wounded surface. In such a case they originate in the cambium layer of the broken root instead of in the pericycle.

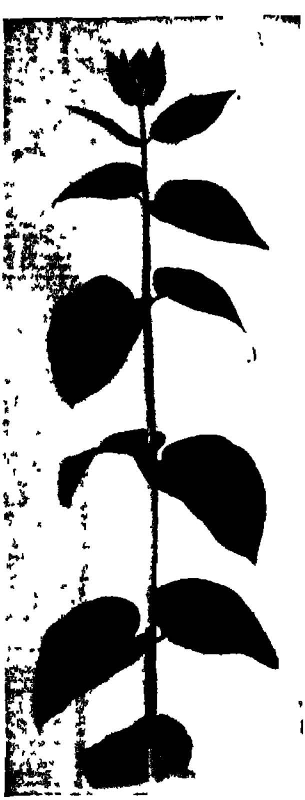


FIG. 81. Terminal shoot of honeysuckle, showing increasing length of the internodes from the tip back toward the base.

Contraction of Roots.—It has often been observed that the crown of a growing plant, i.e., the region where the root joins the stem, is somewhat below the surface of the ground, especially if the ground is soft. It may be that the plant started from a deeply planted seed, but there is in some species another contributing factor. Tap-roots sometimes actually shorten in the portion above the region of elongation. This has the effect of drawing the crown deeper into the soil, as actually happens in dandelions and some other tap-rooted plants. Apparently the contraction takes place through a change in shape of the cells, which become broader and correspondingly shorter.

Elongation of Stems

It is hardly necessary to mark spaces on stems to see, in a general way, where elongation is taking place. The regularly alternating nodes

and internodes serve much the same purpose. At the tip there are three or four nodes so close together that no internodes are visible between them. Below these the nodes become progressively farther apart for a short distance, after which they are rather evenly spaced. From this general observation we learn (1) that most of the elongation takes place in the upper internodes, the actual number varying with the species, and

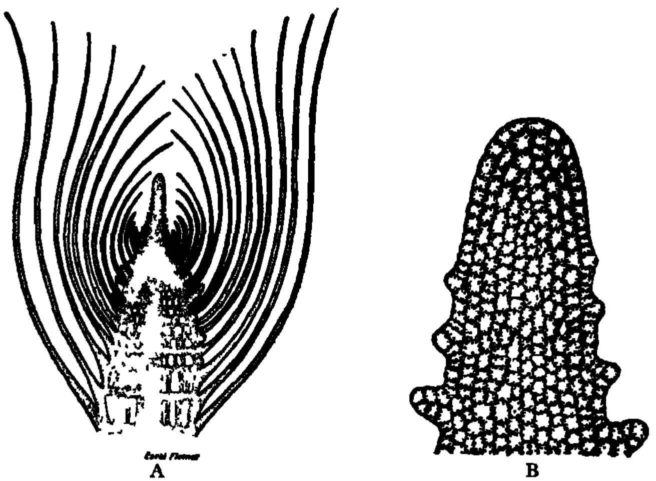


FIG. 82. Stem tip of *Elodea* in longitudinal section. A, nodes with internodes that have not yet elongated. *B, sectional view of extreme tip showing* primordia of leaves and buds. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc.)

(2) that the region of elongation is not nearly so restricted in stems as in roots.

The thorough student, will, however, want to go a step further. He will want to see if any given internode elongates evenly throughout its extent. To determine this, evenly spaced India ink marks may be used as was done on the roots. If this experiment is tried on plants of a considerable number of species, it will be found that there is no fixed rule as to the portion of the node that elongates. Some show greater elongation in the lower part of the internode than in the middle and upper portions, while others elongate evenly. The tendency to elongation of the lower part of the internode for a considerable length of time

is especially noticeable in wheat, oats, and other cereal and grass plants and serves to push the flowering portion well up into the air.

Internal Anatomy.—*In comparing longitudinal sections of root tips* and stem tips one is more impressed with differences than with similarities. There are no structures in stems that are comparable to root-cap or root-hairs. There is a meristematic region, to be sure, and below it a region of elongation and a region of maturation, but these are some-

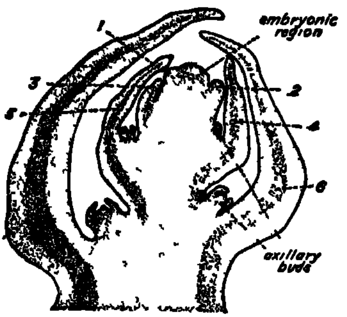


Fig 83 *Longitudinal section* of the stem tip of Dutchman's pipe, showing the formation of buds in the axils of leaves. Diagrammatic (Reprinted by permission from *Text-book of General Botany*, Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc)

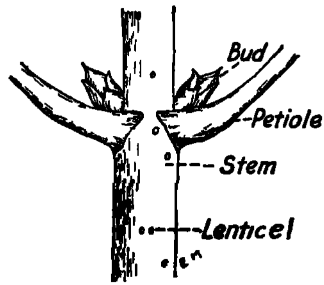


Fig 84 Node of buckeye stem, showing normal position of buds in the axils of leaves

what obscured by the development of leaves and buds that later mark the nodes. The growing point of a stem is protected usually by leaf scales or by foliage leaves. It is made up of a mass of undifferentiated meristematic cells, all potentially capable of division and growth.

In stem tips, as in root tips, a meristematic region adds more phloem and xylem to the ends of the primary fibrovascular bundles, causing them to elongate as the plant grows.

Origin of Leaves and Branches.—Branch stems originate very differently from branch roots. Just back of the growing tip, tiny knobs are plainly visible on the surface of the stem. Under the microscope these are seen to arise by division and growth of epidermal cells. By studying these progressively downward from the tip to the region where they are older, it is discovered that some are the beginnings of leaves and others, appearing slightly later and just above them, are the be-

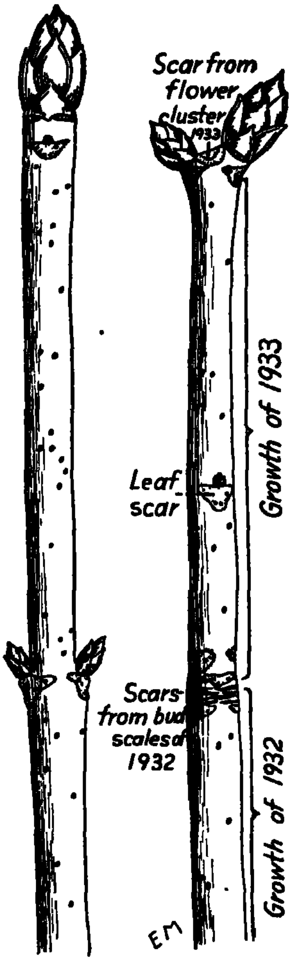


FIG. 85. Dormant twigs of buckeye, showing large scaly buds, leaf scars, and lenticels. At the tip of the right-hand twig is a scar where a flower cluster was produced and farther down is a ring of scars where bud scales fell off. This marks the boundary between the growth of 1932 and that of 1933.

ginnings of branches. Such rudimentary structures are termed *primordia.* They mark the newly formed nodes, each of which has at least one leaf primordium with the primordium of a branch close above it. As the stem elongates, new leaf and branch primordia appear above

FIG. 86. Stems of apple tree, showing external view of lenticels.

the older ones, leaves never forming except as the stem that bears them elongates.

To get a clear comprehension of the future development of these rudimentary structures one needs to look at nodes farther down where the leaves are fully expanded and where the internodes have developed. On woody stems, for example, such as buckeye, apple, or willow, a *bud* will be seen close above the attachment of each leaf, i.e., in its axil. This bud, which is more or less covered with bud scales, represents the growing point of a branch stem. The next season it may grow out into a branch.

Method for Determining Age.—The age of different parts of young shoots of woody plants such as those of apple, buckeye, willow, and lilac

can easily be determined in the winter condition after the leaves have fallen. The terminal portion which grew during the last season is smooth and shining, with leaf scars having well-developed buds just above them. At the base of this newest growth is a rough ring or series of rings around the branch, marking the place where the scales of the terminal bud fell off and left scars the previous spring as the shoot developed from it. Below this is another section of the stem with bark not quite so smooth and a little grayer. Some of the buds have developed into branches, and those that failed to do so are generally

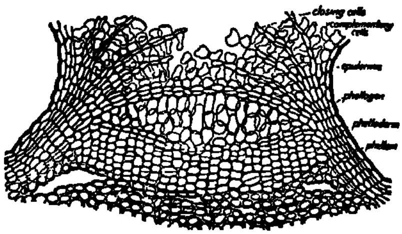


FIG. 87. Section through lenticel of cherry. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Devaux.)

somewhat shriveled. At the base of this section is another ring of scars around the stem. On some trees five or six such successive growths can be recognized, but those older than that have become indistinguishable from each other.

This method is not applicable to roots, where the growth of one season grades imperceptibly into that of the next.

On the bark of both stems and roots of most woody species little corky-looking dots may be seen. They are especially conspicuous in the apple, elderberry, and alder. These dots are *lenticels*, and their porous structure serves to admit air to the cortex and deeper tissues.

Adventitious Structures.—Under field conditions branch stems and roots are not always restricted to the precise place of origin that has just been described. Especially following injuries, new stems and roots may start "out of place," as we say. These are called ***adventitious***. If a branch is cut from a geranium and placed in moist sand, adventitious roots will grow from the cut surface of the end. If a twig of willow in the dormant condition is cut off and placed in water or in wet earth or sand, adventitious roots will start from the lowest buried node or from lenticels on the internodes. Likewise, some plants, such as the

FIG. 88. Adventitious roots. 1, growing from node of wandering Jew; 2, growing from cut end of geranium; 3, growing from lenticels of willow; 4, growing from internode of *Coleus*.

sweet potato, will send out adventitious buds from buried pieces of roots, and the sprouting of many trees from the root is brought about by the development of adventitious buds. However, in the broadest sense, buds growing from stems at internodes and all buds other than those that

FIG. 89. Adventitious buds growing from a sweet potato root in a beaker of water.

started in the axils of leaves should likewise be called adventitious, as should also roots arising at wounds in old roots.

Leaves are never adventitious for they always grow from stems. This furnishes an important method of distinguishing between stems and roots and between leaves and leaf-like stems. Sometimes leaves appear to be borne on roots or on other leaves, but in such cases there is always an adventitious bud which bears the leaves.

Duration of the Growth Period.—Higher animals, when they reach maturity, cease to grow although they may continue to live for many

years. Not so with plants. Generally speaking, they continue to grow as long as they live. Annual plants finish their growth in a few months and then die. The roots of herbaceous perennials add to their growth year after year. Trees hundreds of years old still continue to grow until they succumb to unfavorable environmental conditions.

Should stem elongation not be renewed in deciduous trees after the leaves had fallen, no leaves would develop the following season, for, as already mentioned, leaf development is a sequel to stem development. The tree would then die from inadequate photosynthesis if for no other reason.

Review Questions

1. Explain how cells bring about the growth of plants.
2. Where are the chief growth regions in higher plants?
3. What name is given to cells that are forming new ones by division?
4. Describe an experiment to show what part of a root elongates as the root grows.
5. Starting at the extreme tip of a root and going to the older portion, what five tissue regions will be found?
6. What part of a root-cap is youngest?
7. What is meant by the "region of maturation"?
8. On what part of the root are root hairs formed?
9. Of what advantage is it to a plant to have the root-hairs back of the region of elongation?
10. What happens to the root-cap as it is pushed through the soil?
11. Describe the origin and formation of a branch root.
12. Under what circumstances will branch roots originate in the cambium?
13. How could you tell by a single observation on a young sunflower plant where elongation of the stem is taking place?
14. From what tissue do branches and leaves originate?
15. Where are branches attached in relation to leaves?
16. How would you determine the age of a portion of a branch of a tree without cutting into it?
17. Define (1) adventitious root, (2) adventitious bud, (3) meristematic cell, (4) primary bundle, (5) medullary rays, (6) primary root.
18. How could you cause adventitious roots to start in a stem?
19. How could you regulate the length of the internodes produced by a plant?
20. Roots and stems have lenticels. Why do not leaves need to have them?

CHAPTER X

GROWTH IN DIAMETER

The greatest enlargement of plants is longitudinal. This statement applies to nearly all, even to the low forms in which the plant body is but a single row of cells arranged end to end. The advantages of elongation, enabling the plant to extend upward into the light, are obvious, but it is not so easy to explain why the individual cells enlarge more in one direction than in another. Growth appears to result, in part at least, from the internal pressure of increasing protoplasm, or enlarging vacuoles, or both. It would seem as though such a pressure would cause the cells to become spherical, except as they flatten against neighboring cells. Such a tendency is sometimes evident in the formation of the parenchyma of cortex, pith, etc., but in the region of elongation in roots, stems, and petioles the side walls stretch more readily than the end walls so that internal pressure causes the cells to become elongated rather than round. That growth hormones play a part in the elongation of cells is well established.

ENLARGEMENT OF DICOTYLEDONOUS STEMS

While plant growth is chiefly in the nature of elongation, still there is enough broadening out to justify an investigation of the processes and structures involved.

The Region of Growth in Diameter.—If one studies the character of the bark on the trunk of a dicotyledonous tree such as apple, oak, or poplar, he will notice that it is cracking as though the interior were swelling inside it. He may also observe that no such cracking occurs on the smaller branches nor on the stems of most herbaceous plants. From these observations he can draw two conclusions: (1) that up to a certain point young tissues are adapted to a general expansion of the stem, and (2) that the main region of growth is not at the surface but deeper in than the bark. Indeed, if the growth region were at the surface it could thicken the bark only but could not add to the wood.

The Cambium Layer in Stems.—Brief mention has been made of the cambium layer, made up of cells lying between the phloem and the xylem. This separates the bark, composed of the epidermis, cortex, and phloem, from the xylem which is chiefly wood but may contain a pith in the center. In most trees the cambium is continuous all around the roots and stems, extending nearly to the tips both below and above and in some cases even into the larger leaf veins. In some herbaceous

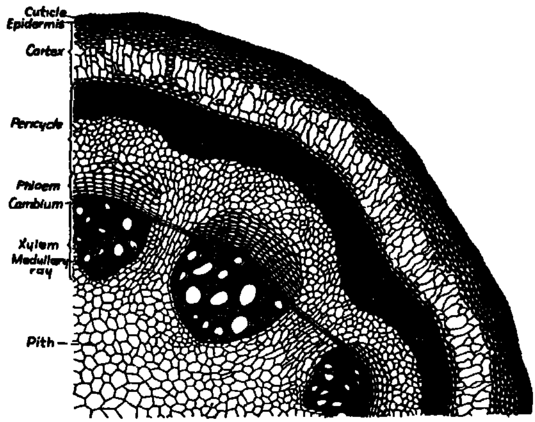


FIG. 90. Sector from cross-section of stem of Dutchman's pipe, showing positions of phloem, xylem, and cambium layer.

plants the vascular bundles are spaced some distance apart, and the cambium does not extend through the spaces between them. Vascular bundles of most monocotyledons and a few dicotyledons have no cambium layer. Those are called *closed* bundles as distinguished from the *open* bundles which possess a cambium.

Seen in a cross-section of a stem the cambium cells are evidently meristematic, for they are closely packed with protoplasm and have large nuclei. Furthermore, stages in nuclear and cell division are frequent. As a rule the cells appear rectangular in shape, and in longitudinal section they are elongated.

The method by which the cambium layer enlarges the stem is very effective. It is one cell in thickness and all the cells undergo division by the formation of walls in the tangential direction, followed by enlargement to the original size. This, of course, would tend to make the layer thicker, were it not for the fact that those cells next the wood

are transformed into xylem elements—vessel segments, wood fibers, wood parenchyma, etc.—while those next the bark are transformed into phloem, including sieve tube mother cells, each of which, by a final division, produces a sieve tube and a companion cell that are sisters. In trees and shrubs the xylem and phloem form layers that are continuous except for their intervening plates of cells, which are the rays. These rays form radial plates in the wood and bark. As the tree grows the

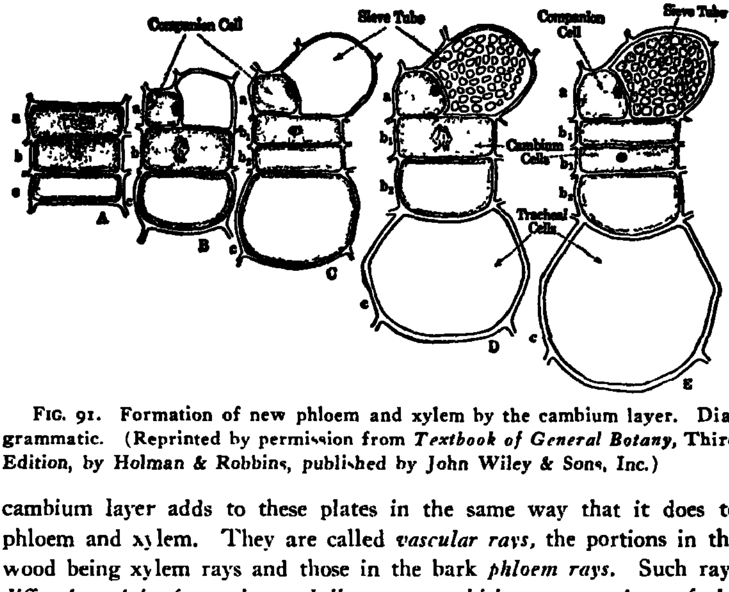


FIG. 91. Formation of new phloem and xylem by the cambium layer. Diagrammatic. (Reprinted by permission from *Textbook of General Botany,* Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc.)

cambium layer adds to these plates in the same way that it does to phloem and xylem. They are called *vascular rays,* the portions in the wood being xylem rays and those in the bark *phloem rays.* Such rays differ in origin from the medullary rays, which are extensions of the pith between the bundles of herbaceous plants, and they must not be confused with them.

It is a matter of common observation that the layer of wood from the cambium to the pith is much thicker than the layer of bark from the cambium to the outside. This is due chiefly to the fact that the cambium produces xylem cells toward the center more frequently than it produces phloem cells on the outside. As the stem enlarges, the wood pushes the cambium layer outward so that it becomes larger and larger in circumference although remaining one cell in thickness. This enlargement of the cambium layer is accomplished by division of its cells in the radial direction, whereas the formation of phloem and xylem ele-

ments results from tangential cell division. From this cambial activity it may be reasoned that the inner bark is younger than the outer, and that the outer wood is younger than the inner.

Character of the New Xylem.—The first fibrovascular strands that form from the meristem of the growing point are designated as *primary* bundles. *Secondary* phloem and xylem are produced by the activities of the cambium layer. The question now arises: Does the cambium merely enlarge the primary bundles already existing or does it make new ones between them? The answer depends on the kind of plant under discussion. In a few slender, perennial vines, notably the moonseed of the South, the number of bundles remains constant, but each increases in size. More commonly, as in the burdock, the primary bundles enlarge by the addition of secondary phloem and xylem, and new additional bundles appear between them Most common of all is a condition, illustrated by foxglove, honeysuckle, and sweet gum, in which the secondary phloem and xylem are not in definite bundles but make a continuous layer in the form of a hollow cylinder.

It should be understood that among the thousands of species of higher plants there is much variation in the details of structure found in the stems and roots, so much in fact, that many kinds of plants can be identified by these parts alone. For example, squash vines and other members of the same family have a small cavity in the center. This is formed, apparently, by growth in circumference of the vascular layer, which enlarges the central space inside it and causes a mechanical disruption of the pith, which has ceased to grow. Each of the fibrovascular bundles around this cavity has a phloem region on the outside, next the cortex, and another on the inside, next the central cavity, with a xylem region between the two. This type of bundle is called *bicollateral* as distinguished from *collateral* bundles which, like those described in Chapter VII and earlier in this chapter, have a single phloem region outside the xylem.

Formation of Annual Rings.—Annual rings of growth are a familiar sight on logs, firewood, lumber, and furniture. In analyzing their nature a lesson in growth is learned. If a cross-section of wood is examined with a strong hand lens or with the low power of a microscope, it will be seen that each ring is made up of large and small cells having walls of different thicknesses. The rings vary considerably with the species, but the tendency is for the inner cells of each ring to be larger and thinner walled than the outer ones. The larger vessels are produced in the spring, when growth is most active, and the smaller

ones as the season advances and growth slows down. In regions of uninterrupted summer growth alternating with a dormant winter period, these rings form an accurate index to the age of a tree. In other regions this index may be made unreliable by periods of summer drought or by continuous growing conditions the year round.

Most of our trees are dicotyledonous and form annual rings through the activity of the cambium layer. The palms, however, are monocotyledonous, with scattered bundles and no cambium layer. As would be expected, they do not form annual rings of growth.

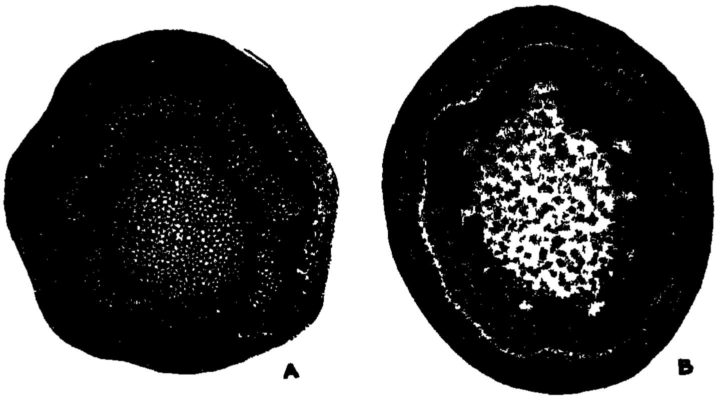


FIG. 92. Secondary growth of phloem and xylem. A, sycamore tree, with stele in the form of separate bundles; B, honeysuckle vine with stele in the form of a continuous hollow cylinder. (From Sinnott & Bailey, *Annals of Botany*, Volume 36.)

Healing of Wounds.—When a branch is cut off from a dicotyledonous tree, or a wound is made through the bark, the cambium layer around the margin of the wound forms wood and bark that extend inward until the wound is healed over.

Roughening of the Old Bark of Trees.—One of the most conspicuous features of the bark on the trunk of an old tree is its rough, shaggy appearance. It looks as though it were being split in many places. Such is actually the case. As new phloem and xylem are formed by growth in the cambium region the stem becomes larger in diameter. The epidermis and cortex expand for a time by the enlargement of their cells and the occasional division of cells here and there but not in a definite growth region. In small plants no other adjustment is necessary. In

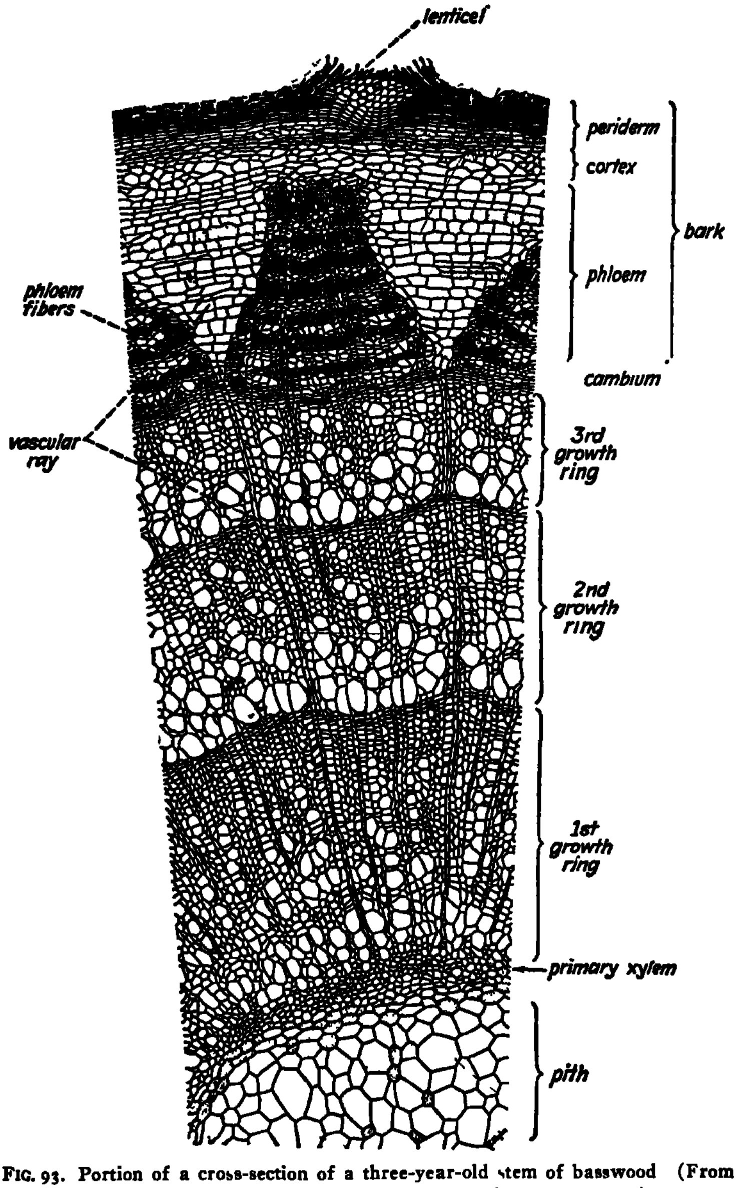


FIG. 93. Portion of a cross-section of a three-year-old stem of basswood (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

larger trees, however, such expansion is insufficient, and extensive vertical splitting of the bark takes place.

Several agencies contribute to the formation of the bark of a tree or shrub. The primary structure consists of the phloem surrounded by cortex and epidermis. Some months later, or the following season,

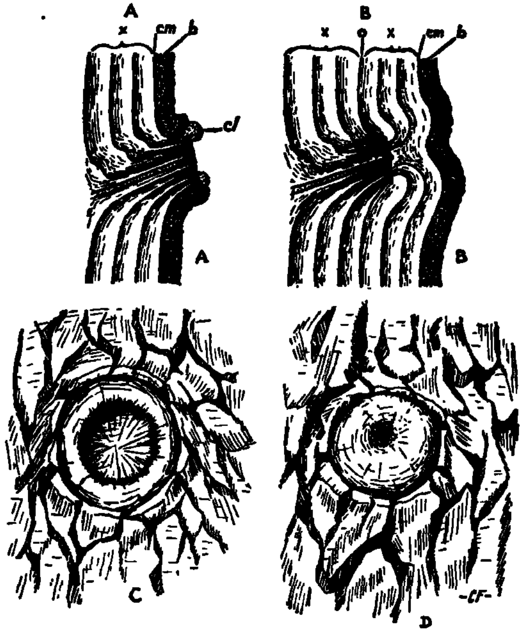


FIG. 94. Healing of wounds by growth from the cambium layer. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

there forms a smooth, thin, outer layer of cork which replaces the epidermis. This is easily studied on apple and birch trees, for example, where it can sometimes be peeled off in a thin sheet. This and other formations of cork that appear later are produced by cork cambiums that originate in the pericycle, cortex, or epidermis. The walls of the cork cells are impregnated with ***suberin***, which makes them almost impervious to the passage of water and serves to check evaporation. Later, other corky layers are produced in the pericycle or even in the phloem, and these shut off the supply of water and food to the epidermis and cortex. These tissues then die and disappear before the trunk attains

much size. As splits appear in the outer bark from internal growth, healing takes place through the formation of more cork in discontinuous patches. The rough bark of an old tree is made up of a thick layer of functional phloem next to the cambium, surrounded by a dead outer portion that is a mixture of non-living phloem and cork with no outer layer of cortex and no epidermis, these tissues having been lost by weathering.

The cork oak found in Spain and some other countries forms a thick, even layer of cork that may be removed without serious injury to the tree and has considerable commercial value for making bottle stoppers, etc. This tree then restores the layer of cork, which may be removed at intervals of a few years for a long period of time.

Growth in Diameter of Monocotyledonous Stems

There has been much study of the growth in diameter of dicotyledonous stems, the details of which vary considerably in different herbaceous and woody plants. Monocotyledonous plants have received less attention, largely because most of them are herbaceous and of relatively small size or grow in the tropics where extensive botanical studies have not been made. More or less growth does take place in all of them, however, and this may take any of three forms: (1) the formation of relatively small, solid stems like those of corn and sugar-cane; (2) the formation of small, hollow stems like those of wheat, oats, and most grasses; and (3) the formation of tree trunks a foot or more in diameter.

In corn stems the region of maturation near the growing tip produces fibrovascular bundles interspersed with parenchyma which fills the spaces between them. These primary bundles are numerous and serve the purposes of the plant throughout its lifetime, no secondary bundles being formed. The stem grows in diameter by the enlargement of cells, chiefly those of the parenchyma between the bundles. This cell enlargement is brought about, for the most part, by the development of central vacuoles.

In hollow stems the vascular bundles are arranged near the periphery and no parenchyma forms in the center, or, if it does form, it breaks down early as the outer layer expands, leaving a cavity filled with air. Growth in the peripheral layer is brought about by the enlargement of cells and is very limited except in a few large species, such as bamboo.

In some of the monocotyledonous trees, the aloe, Joshua tree (*Yucca arborescens*), and dragon tree (*Dracaena*), and in some species of palms,

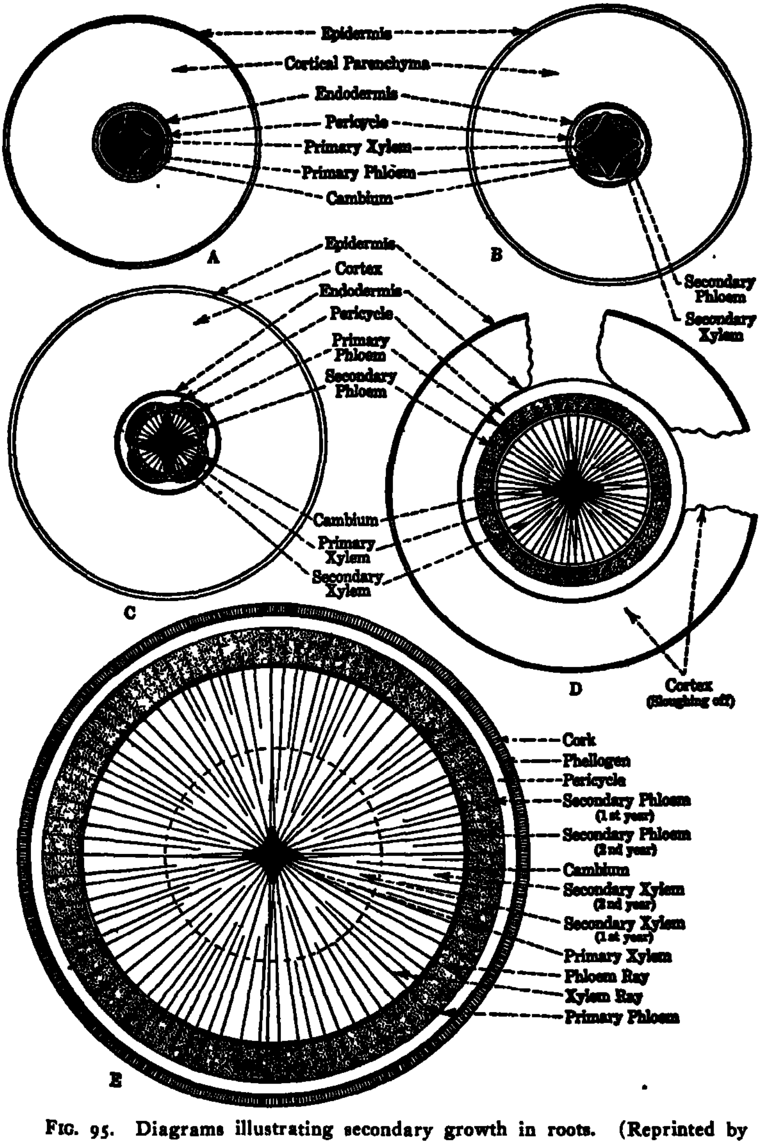


FIG. 95. Diagrams illustrating secondary growth in roots. (Reprinted by permission from *Textbook of General Botany*, Fourth Edition, by Holman & Robbins, published by John Wiley & Sons, Inc.)

the trunk attains considerable size—a foot or more—and growth in diameter involves the addition of secondary fibrovascular bundles. To accomplish this, some of the cells of either the pericycle or the inner cortex divide and thus form a discontinuous cambium layer. Of the newly formed cells, some are differentiated into the phloem and xylem of new vascular bundles, forming a layer outside the primary bundles, while others form parenchyma or sclerenchyma cells between and out-

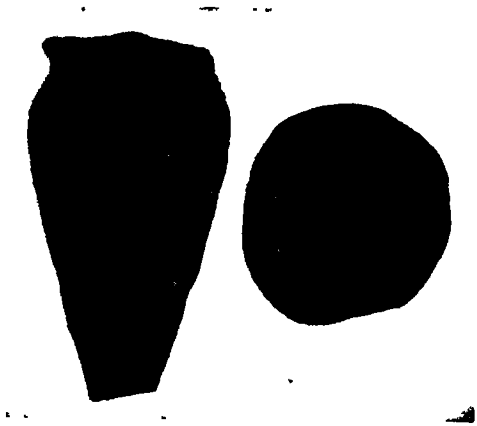


FIG. 96. Fleshy root of sugar-beet, with conspicuous rings of growth formed by a series of cambium layers that develop successively from the pericycle.

side them. This process goes on throughout the remainder of the life of the plant. One speciman of the dragon tree is estimated to be six thousand years old and has a diameter of 15 feet.

Enlargement of Roots

The method by which roots grow in diameter has much in common with that occurring in stems.

Primary and Secondary Bundles.—In their primary structure roots differ from stems in the relative positions of phloem and xylem. In a young root the primary phloem does not lie in a radial direction outward from the xylem as in a stem, but the phloem bundles lie between the xylem bundles, often with both touching the pericycle. In other words, the phloem and xylem alternate with each other. As in the stem, the cambium layer, when it forms, lies between phloem and

xylem. In such a position it curves inside a phloem bundle, then outside a xylem bundle, and so on around.

In the formation of secondary bundles, however, the convolute form of the cambium layer is straightened out. The secondary phloem is produced as an inward continuation of the primary phloem, but the secondary xylem does not develop as a continuation of the primary xylem. On the contrary, it is produced radially inward from the phloem as in

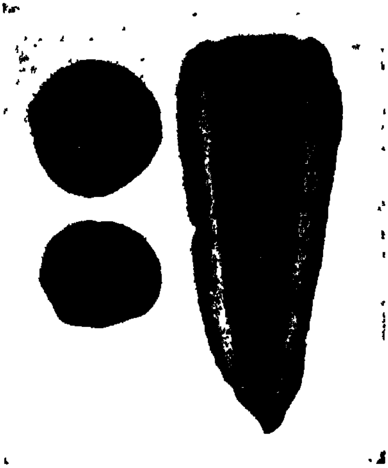


FIG. 97. Fleshy storage root of carrot.

stems. This secondary xylem is some distance inward from the cortex, but it is above the functional root-hairs and comparatively little soil water enters it here through the cortex. The separation of the two tissues is, therefore, unimportant.

Development of Fleshy Roots.—A study of the enlargement of fleshy roots brings to light some interesting modifications of the usual method of growth in diameter. In the first place only a small proportion of the root is made up of sieve tubes and xylem vessels. For the most part fleshy roots are made up of large storage cells.

In the beet there are several cambium layers arranged concentrically. The activities of these several cambiums result in rings of growth somewhat resembling in appearance the annual rings of a tree but differing fundamentally in that each ring contains both xylem and phloem, and all form in a single season.

Review Questions

1. Name the chief regions in plants where meristematic cells are found.
2. Describe the way in which the cambium layer adds to the phloem and xylem.
3. Explain how growth in diameter takes place in monocotyledons such as corn.
4. How does it take place in large monocotyledonous trees such as the dragon tree?
5. Where is the oldest part of the phloem? Of the xylem?
6. In what three ways are the new phloem and xylem formed?
7. Explain the structure and formation of annual rings in trees.
8. Under what conditions could two annual rings form in one year?
9. What is the difference between the sap-wood and the heart-wood: (1) in location, (2) in general appearance, (3) in physiology, (4) in structure?
10. What is the distinction between medullary rays and vascular rays?
11. Do vascular rays grow? If so, how?
12. What is the distinction between primary and secondary phloem and xylem?
13. Describe the arrangement of primary and secondary phloem and xylem in roots.
14. Give the chief morphological difference between the beet root and the carrot root.
15. Give the functions of the following: (1) root-cap, (2) root-hairs, (3) xylem, (4) phloem, (5) fleshy root.
16. What causes the old bark of a tree to be so rough?
17. Explain the absence of epidermis and cortex from the bark of an old tree.
18. In regions where the wind is mostly from one direction, why is the bark on the windward side of the trees smoother than that on the leeward side?
19. What makes the layer of wood from the center to the cambium so much thicker than the layer of bark from the cambium to the outside?
20. Why does not a monocotyledonous tree form annual rings?
21. Give evidence that tree roots can exert great power by their growth in diameter.

Part Five

REPRODUCTION IN PLANTS

CHAPTER XI

THE CELL IN REPRODUCTION

No aspect of botanical or zoological science deserves more careful study than reproduction. No biological study brings one into contact with more remarkable phenomena. Through the processes of reproduction not only is the species continued and the number of individuals increased, but the characteristics of the offspring are determined.

Reproduction is intimately associated with cell division. All living things, regardless of size, have small beginnings. In the sexual reproduction of plants and animals two cells, both produced by cell division, unite to form one cell, which is the first stage of the offspring. Most lower plants have also another method by which one cell alone can start a new plant and, as many such cells are quickly formed, the method is very rapid. In either case cell division segregates from the parent a bit of protoplasm that determines the inherited characters of the offspring. As the new individual grows and develops, its cells divide, and those that are newly formed inherit the characters of the old. Thus from cell to cell the inherited tendencies are handed down.

Many researches have pointed to the conclusion that the nucleus is the cell organ that passes on the inherited tendencies from old cells to young, from parent to offspring.

DIVISION OF THE NUCLEUS

Cell division is a preliminary to growth, but more significant is the fact that it is the method by which cells are reproduced. When a cell is to divide and make two, it necessarily follows that if it has only one nucleus, as is usually the case in higher plants, this nucleus must first divide into two, or else one daughter cell will be lacking a nucleus. As a rule, then, nuclear division is a preliminary to cell division.

Structure of the Nucleus.—To comprehend the remarkable mechanism that has been set up for the division of the nucleus, it will be necessary first to see exactly what has to be divided. The nucleus is not just a lump of granular material; it is a highly organized struc-

ture of vital significance. The term *resting* nucleus is applied to one that is not at the moment dividing. This must not be construed to mean that the nucleus is not functioning, for in the life of a plant the nucleus carries on other work of importance besides division.

Bounding the resting nucleus is a thin, transparent *nuclear membrane* that preserves, somewhat, the shape of the entire body. Inside this membrane are numerous tiny bodies made of *chromatin* material. There is evidence that each of these contains numerous still smaller bodies, *genes,* but these cannot actually be seen and their morphological character is still undetermined. The visible chromatin particles seem to be loosely connected by a network of *linin threads.* Sometimes there is also a conspicuous lump, the *nucleolus,* but it is not of regular occurrence and seems to be merely a storage body.

The Mitotic Process.—The term *mitosis* is applied to the nuclear division here described. As mitotic nuclear division, considered in all its details, is a somewhat complicated process, only the main features will be considered here, but a preview of what is accomplished by it will make it more intelligible. Evidence points to the conclusion that it is through the genes of the nucleus that the inherited traits of the offspring and, indeed, of each individual cell are determined. There appear to be very many genes in each nucleus, each differing from the others in the part it plays in inheritance. Normal mitotic division accomplishes with great accuracy the difficult feat of dividing each gene and including half of it in one daughter nucleus and half of it in the other. As a preliminary to nuclear division the chromatin particles are gathered into groups, probably through the action of the linin threads. The groups are vague in outline, never clear-cut, and are often indistinguishable. They are called *chromosomes,* and there is a definite number in each nucleus, a number which is always the same for each species of plant. By further contraction of the linin these chromosomes are drawn together end to end and, in some cases at least, appear to form a continuous spireme thread in which the individual chromosomes usually are no longer recognizable. The behavior of the chromatin bodies at this stage is difficult to follow, and some investigators question the earlier accounts of the formation of one continuous spireme thread, holding, rather, that there are several shorter strands of chromatin. It is possible that the nuclei of different kinds of plants behave differently in this respect. The chromatin material, whether a single strand or several, now splits lengthwise, and it is presumable that in this

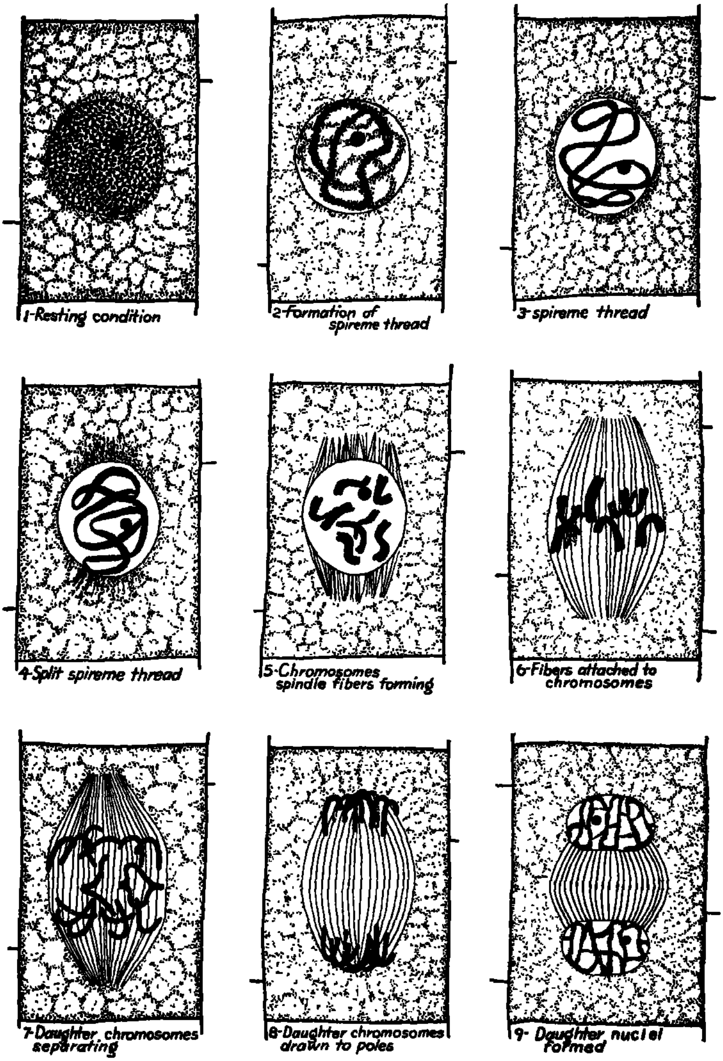


FIG. 98. Nuclear division by mitosis. 1, resting condition prior to mitosis; 2 to 5, prophases; 6, metaphase; 7 and 8, anaphases; 9, telophase. Somewhat diagrammatic.

process every chromatin body and every gene is divided in two. Transverse division now breaks up the spireme thread into its distinct chromosomes, which by this time have become compact and definite.

Meanwhile, some of the denser protoplasm has become arranged into two fibrous *polar caps* placed opposite each other on the outside of the nuclear membrane. The nuclear membrane now disappears and the material from the polar caps extends into the interior of the nucleus in the form of *spindle fibers,* some of which extend from each pole to the split chromosomes. By an unexplained discrimination the fibers from one pole become attached to one set of daughter chromosomes and those from the other become attached to the other set of chromosomes. Thus two sister chromosomes are never, under normal circumstances, connected to the same pole. By contraction of the fibers one set of chromosomes is now drawn to one pole while the other set is drawn to the other pole. There is evidence that the hereditary possibilities of the two sets are practically identical. A nuclear membrane is now formed about each daughter nucleus, its chromatin becomes dispersed as scattered particles characteristic of the resting nucleus, and the process is complete.

In such a method of nuclear division we see greater significance than merely providing two nuclei for two daughter cells. By this mitotic process a qualitative as well as quantitative division of the nucleus has been accomplished. Each portion of the chromatin has been divided evenly, and thus each daughter nucleus is essentially like the mother nucleus and like its sister nucleus. The new cells are thus provided with nuclei that will guide their destinies in the paths of their ancestors and determine their behavior under a wide variety of conditions.

If the reader thinks that this is a complicated process let him try to devise a simpler one that will make a quantitative division and separation of all the genes, using only the machinery found in a nucleus.

While the term "resting" has been applied to nuclei that are not in the process of division, this term is somewhat misleading. If nuclei are responsible for causing the offspring to resemble the parent in structure and behavior, as appears to be the case, they must exert an influence upon the cells that contain them during the time when they are not dividing. Furthermore, from the position and behavior of "resting" nuclei in active cells one is led to believe that they are in some measure directing the physiological processes carried on by the cell. The early death of some cells, such as an ascus after the nuclei have all been in-

cluded in ascospores by free cell formation (see pages 158 and 286), suggests the importance of the nucleus even though it is not dividing.

Amitotic Nuclear Division.—Mitosis as just described is found in all plants, or nearly all, both higher and lower. In a few diseased or unhealthy cells a less exact method of nuclear division may take place. The nucleus in the resting condition is pulled into two parts, not necessarily of equal size, and there is no mechanism for segregating the

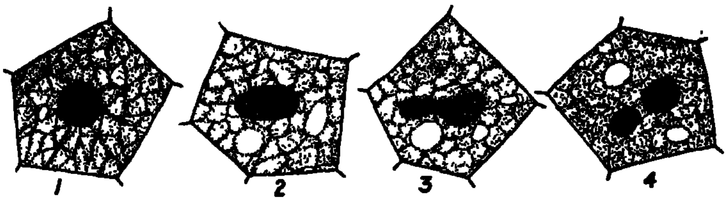


FIG. 99. Nuclear division by amitosis. Somewhat diagrammatic.

chromatin bodies equally. Such cells soon die or at least never enter into the reproduction of the plant.

DIVISION OF THE CELL

While nuclear division follows the same plan in all, or nearly all, normal plants, cell division presents more variety. Higher plants have one kind and lower plants have several other kinds. Altogether, five kinds of cell division are known in plants.

Division by Cell Plate.—In higher plants nuclear division usually is followed so closely by cell division that the same mechanism is used for both processes. When mitosis is complete there still remains between the daughter nuclei a mass of spindle fibers. These now proceed to divide the cell. Their ends withdraw from the nuclei, and the fibers thicken in the equatorial plane of the spindle midway between these nuclei. Here they swell out to such an extent that they come in contact with each other and fuse, thus forming a continuous *cell plate* into which they are entirely absorbed. As the fibers are drawn more completely into the cell plate, it widens at its margins until it reaches the old cell wall. The plate now splits throughout its entire extent, usually beginning at the center. In the rift thus formed a new wall is laid down which completely divides the mother cell. It will be noted that the cell plate is not a cell wall. It is protoplasmic in nature and becomes the plasma membrane on each side of the new wall.

Cell Division in the Lower Plants.—Reproduction in lower plants is much simpler and more easily comprehended than it is in higher plants. It seems well, therefore, in advance of the detailed chapters on this part

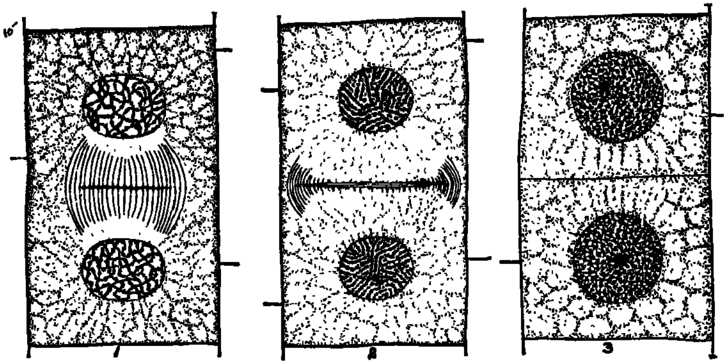


FIG. 100. Division of cell by cell-plate method. 1, spindle fibers contracting and forming cell plate; 2, new cell wall forming in split of cell plate; 3, new wall completely formed. The cell plate has become the plasma membranes next the new wall. Somewhat diagrammatic.

of the plant kingdom, to describe some of these processes. The lower plants here referred to are bacteria, yeasts, molds, and algae. Some of these plants are microscopic one-celled organisms. The plant body of others is a thread-like chain of cells, often much branched. In most of

FIG. 101. Division of cell by constriction. By this means cells are increased in number in the thread-like bodies of the lower plants. (Redrawn from Edna M. Lind, *Annals of Botany,* Volume 46.)

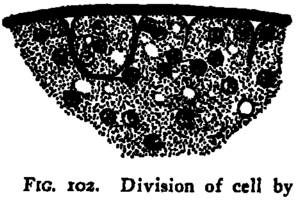


FIG. 102. Division of cell by cleavage. A relatively large cell of the bread mold, containing many nuclei, is being divided into reproductive spores by cleavage furrows cutting inward from the surface.

these forms, perhaps all, nuclear division is by mitosis. As a rule nuclear division is not followed immediately by cell division, and the spindle fibers take no part in the division of the cell.

The simplest known method of cell division is by *constriction.* It occurs in all these lower plants. In constriction the plasma membrane contracts to form around the cell a ring-shaped furrow that pinches the protoplast in two. If the wall is very plastic it bends inward with the plasma membrane. If it is rigid it retains its shape and a new wall is formed in the constriction furrow, starting at the outside and extending progressively toward the center.

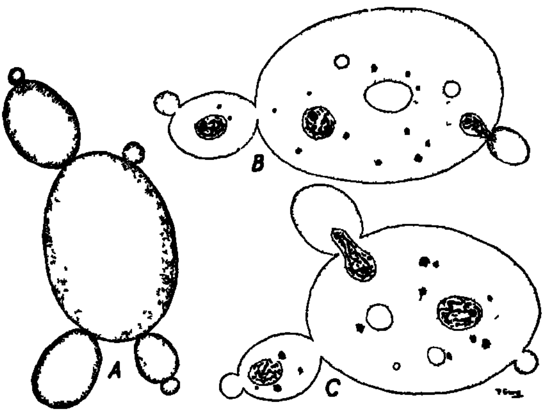


FIG. 103. Division of cell by budding. One-celled yeast plants are reproducing by this method. The final step is the cutting off of the buds by constriction. A, external. B and C, internal. Somewhat diagrammatic.

In the common bread mold one method of reproduction is by one-celled *spores,* each capable of growing into a new plant. These spores are produced inside a spore case. The spore case is at first a relatively large cell, visible to the naked eye and containing dense cytoplasm and hundreds of nuclei. This big protoplast is divided into many spores by a process of *cleavage,* which is similar to constriction but differs in that several furrows cut into the cell simultaneously, thus carving out bits of protoplasm that are the reproductive spores.

Yeast plants are one-celled and form new cells by *budding.* The cell wall softens at some point, and internal pressure forces a little cytoplasm out in the form of a tiny knob or bud. The nucleus divides and one of the daughter nuclei passes into this bud, where it continues to grow larger. It is still connected with the mother cell by a narrow neck which is finally severed by constriction. Budding, then, might be considered a form of constriction, but it differs sufficiently in its early stages to be entitled to a separate name.

Lastly, a unique process of cell division has been found in certain mildews and related fungi Here a sac is formed, containing eight nuclei which are to become the centers of eight spores Each nucleus has a beak extending from it, and at the tip of this is a mass of delicate fibers radiating in all directions These fibers fold around a bit of the cytoplasm enclosing the nucleus and thus carve out a one-celled spore. The

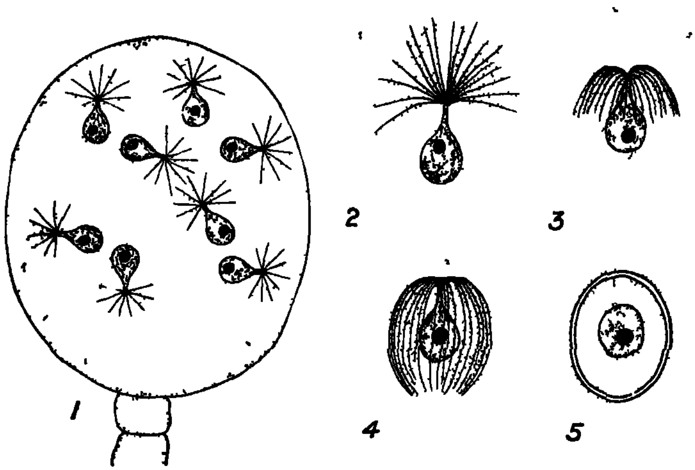


FIG 104 Division of the cell by free cell formation In this unique process found only in one class of fungi fibers from a beak of the nucleus fold around the nucleus, thereby cutting out a reproductive spore Somewhat diagrammatic

cytoplasm of the ascus outside the spores is thus left without a nucleus and soon dies This kind of cell division is termed *free cell formation*

We thus have five recognized methods of cell division, one in the higher plants and four in the lower plants

SIMPLE REPRODUCTIVE BODIES

In the lowest one celled plants reproduction is through simple cell division by constriction One individual forms two, the entire body of the parent becoming incorporated in the offspring, and nothing is wasted.

A little higher up in the scale of life, where the plant body is in the

form of branching threads, spores (usually one-celled) are pinched off the ends of certain branches by constriction or are produced inside spore-cases by cleavage. Each of these spores is capable of germinating and growing directly into a new plant all by itself. This process in which there is no union of reproductive cells is called *asexual*, or *non-sexual*, reproduction in contrast with the next to be described.

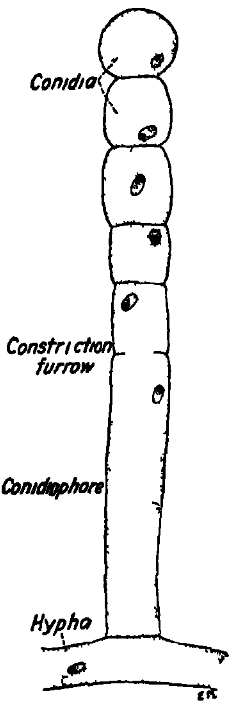


FIG. 105 Asexual reproduction in a mildew One-celled spores are being pinched off from stalks by constriction.

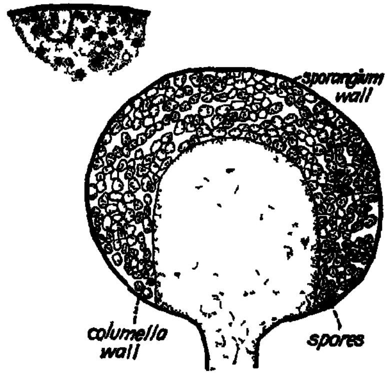


FIG 106 Asexual reproduction in bread mold Spores have been produced in this spore-case by cleavage.

CONJUGATION

An almost universal method of reproduction, one found in nearly all plants and animals, involves the union of two cells that are usually unrelated. Such cells are called *gametes* and the process of their union is *conjugation*. In some cases these gametes are very ordinary-looking

cells, but in others, especially in the higher plants and animals, they are very much specialized. In any case, they have a strong physiological tendency to unite with each other so completely that one cell is formed from two. The final and most essential step in the process is the conjugation of the gamete nuclei. The new cell thus formed is a *zygote*. It is the beginning of a new plant. In many plants and most animals one individual contributes one gamete and another individual contributes the other. Long before this process was understood it was named *sexual* reproduction. It involves the intimate union of two gamete cells as contrasted with asexual reproduction in which there is no such union. Generally the gametes differ considerably in size and appearance. The male gamete is likely to be small and capable of active movement. The female usually is larger, with more stored food, and is relatively inactive.

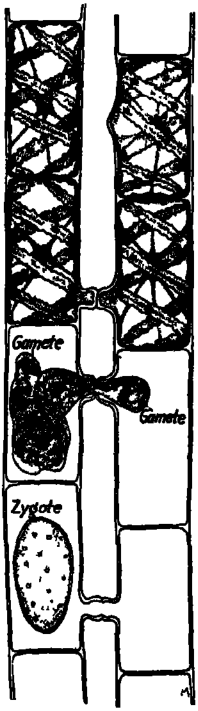


FIG. 107. Sexual reproduction. In this low, green, water plant (*Spirogyra*) a reproductive gamete unites with a similar gamete of a neighboring plant and conjugates with it, thus forming a zygote, which later develops into a new plant.

Quite commonly plants have both asexual and sexual reproduction.

Significance of Asexual Reproduction.—Reproduction by asexual spores serves the purpose of rapid increase. For example, in the course of a few days many thousands of such spores are formed by a single plant of the green mold so commonly found on spoiling fruit.

Significance of Sexual Reproduction.—Sexual reproduction is generally a slow process. If numerical increase were the sole object of reproduction it could well be dispensed with and the whole responsibility thrown onto the other method. However, the fact that the sexual method is the more universal of the two in animals and is almost as universal in plants suggests that it has some great significance.

Some years ago it was thought that rejuvenation or reinvigoration was the result attained by the conjugation of unrelated gametes. However, among the lower plants there are some groups that have no conjugation and yet show no lack

of vigor. Experimentally, one-celled animals have been made to reproduce by simple cell division without conjugation for hundreds of generations with no indication of degeneration. Even some higher plants like the potato, apple, banana, sugar-cane, and pineapple, that have been propagated for centuries without seeds, remain vigorous. Evidently we need to look elsewhere for the advantage gained by conjugation.

Much evidence points toward some aspect of heredity for the answer. It has long been known that the traits of both parents are represented in the offspring. More recently it has been found that the

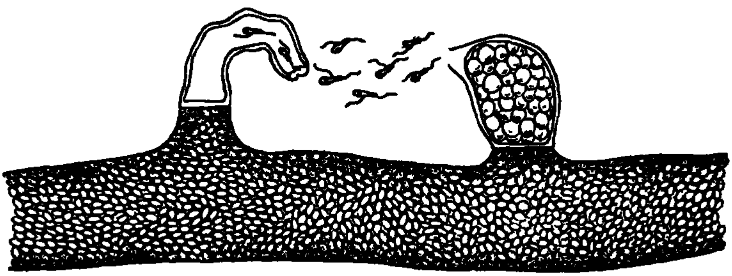


FIG. 108. Sexual reproduction in a low, green, water plant (*Vaucheria*). Here a tiny, motile, male gamete unites with a larger, non-motile, female gamete.

nucleus chiefly bears the responsibility for the continual reappearance of these traits in the next generation. Nuclear fusion is an essential climax in conjugation. An *individuality* is now recognized in chromosomes, each being different from the others and maintaining its identity. Lastly, it has been shown that in nuclear fusion the *chromosomes themselves conjugate* and mate in a very definite way. This evidence points to benefits derived through a blending of parental traits accomplished by conjugation and through the initiating of a tendency to variation in the offspring. It has been observed that offspring originating by the sexual method are more likely to show variation from parental characters than those originating asexually, and this tendency makes possible improvement by evolution, if the variation is of a kind that is beneficial.

Maintenance of the Chromosome Number

A definite number of chromosomes in the nucleus is characteristic of each species. There may be as few as four or there may be many times that number. It can easily be seen that when two gametes fuse

the number will double There must be some method of reduction to the original number or in time there would be myriads of chromosomes in each nucleus It might be reasoned that when the nuclei fuse, the number in the zygote becomes the same as that in each gamete However, cytological studies have shown that in plants, as a rule, the chromosomes do not unite as soon as they are brought together by nuclear fusion For a time, then there will be a double number Indeed, in some plants nuclear and cell division may go on for weeks before the number is reduced to that of the gamete It is customary to speak of the single number of chromosomes as *haploid* and the double number as *diploid* For convenience these are often referred to as *n* chromosomes and *2n* chromosomes, respectively instead of stating the specific numbers as seven and fourteen, for example In each species of plant, however, there is a definite stage in development at which the diploid number is reduced to the haploid In later chapters on the different groups of plants this stage will be referred to The number of chromosomes is not reduced simply by their conjugation but by a process presented in Chapter XXV

Review Questions

1 What organ of the cell determines chiefly the characters of the daughter cells resulting from its division?
2 What is the advantage in having all parts of the chromatin of a nucleus equally divided in nuclear division?
3 Why is this necessary in somatic cells that do not enter into the reproduction of the plant?
4 Describe in detail the process of mitosis or indirect nuclear division
5 In what different plants is it found?
6 Describe the process of amitosis or direct nuclear division
7 In what different plants is it found?
8 In what respect would amitosis fail to serve the needs of a plant as a regular method of nuclear division?
9 Name five kinds of cell division
10 Where in the plant kingdom is each found?
11 Describe each in detail
12 What is a spore?
13 Name three ways that spores are formed
14 Explain how a spore forms a new plant
15 What is a gamete?
16 How are new plants formed by gametes?
17 Name the several steps in the process of conjugation
18 What effect does conjugation have on the chromosome number of the nuclei?

19. Give three ways of expressing the chromosome number of a gamete. Of a zygote.
20. What is meant by the "individuality" of chromosomes?
21. How many kinds of reproduction do most plants have? Name them.
22. Give the special advantages of sexual reproduction.
23. Give the special advantages of asexual reproduction.
24. What is the evidence that the material in the spindle fibers is very similar to that in the plasma membranes?
25. Try to devise a method of nuclear division by which all parts of the nucleus would be equally divided and that would be simpler than mitosis as we know it.

CHAPTER XII

FLOWERS IN REPRODUCTION

Many elaborate structures have been evolved for insuring that reproduction shall take place in an effective way. Of these structures the

FIG. 109. Flower of St. John's-wort (polypetalous). The organs of this flower are unusually well exposed to view. Left, external view; right, median longitudinal section.

flowers of higher plants are the most conspicuous and have received the most attention.

The Flower of St. John's-wort.—A flower that is particularly suitable for study is that of a large-flowered species[1] of St. John's-wort, that is native to the southern states and is grown in greenhouses else-

[1] *Hypericum chinense* is the botanical name of the plant here described and shown in figure 109.

where. It is nearly two inches in diameter and rich yellow in color, with very distinct parts.

The stalk, or *peduncle*, of a flower is really the terminal portion of a stem. Its extreme tip is more or less expanded to form the *receptacle*. Peduncle and receptacle are specialized parts of the stem and bear the other organs, which are specialized leaves.

The green outer leaves that enclose the other parts in the bud are *sepals*. The whole collection of sepals is the *calyx*. The yellow, showy leaves are the *petals*. Collectively they make up the *corolla*. Still far-

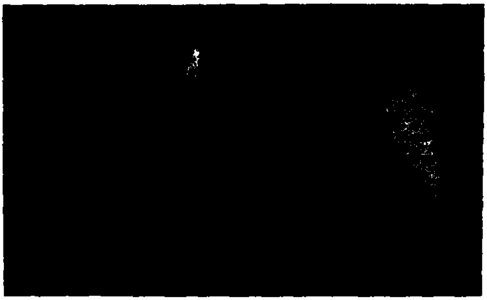


FIG. 110. Flower of morning glory (sympetalous). In this flower the five petals are united into a bell-shaped corolla.

ther toward the center are numerous *stamens*. These are highly specialized leaves that produce *pollen grains*. The stalk of a stamen, corresponding to the petiole, is the *filament*, and the spore sac on top, corresponding to the blade, is the *anther*, within which numerous pollen grains are formed. In the center of the flower is the *pistil*. In St. John's-wort it is composed of five *carpels*, which are specialized leaves firmly united to each other. The swollen base of the pistil is the *ovary*. Extending upward from it is a slender *style* bearing on its top the *stigma*, a somewhat rough and sticky organ suitable for the reception of the pollen grains.

Within the chambers of the ovary are numerous tiny *ovules* which, when they develop, become the *seeds*, while the ovary enclosing them becomes the *fruit*. Each ovule contains a female gamete, or egg cell, the formation of which is a complicated process described in Chapter XXIV.

As the flower matures the anthers open and shed their pollen grains, many of which are lost, but some of which reach the stigma of the same or other flowers. Here they germinate and send tubes down

through the style into the ovary, where they penetrate the ovules and reach the egg cells. A male nucleus now unites with the female nucleus in each ovule and this fertilized egg cell then develops into an embryo plant. The ovule thus becomes a seed containing an embryo plant. Shortly after pollination the petals and stamens wither and die.

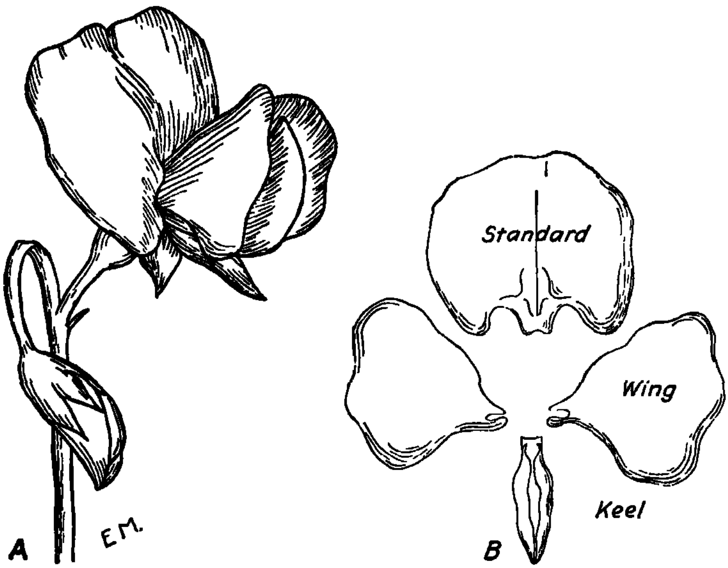


FIG. 111. Flower of pea (irregular). A, perspective view; B, petals removed from flower.

The Flower of the Morning Glory.—The morning glory flower has the same floral organs as St. John's-wort but differs in certain details. The stamens are fewer—only five—and the petals are not separate from each other but are united, edge to edge, thus forming a bell-shaped corolla. It must not be supposed that these petals formed separately and then united. They originated in one continuous corolla.

The Flower of the Pea.—In the pea flower the corolla is much more specialized. No two petals are exactly alike. The large upper one is the *standard.* At each side of it is a *wing* petal, the two wings being similar but with right and left formation. Below these, and folded inside them in the bud, is the *keel.* While the smallest of all, it is really made up of two similar petals that are united at one margin.

This flower, then, while apparently four-petaled is really five-petaled. The pistil consists of a single carpel which develops into a pod.

Floral Types.—The flowers just described illustrate some of the commoner variations in structure.

FIG. 112. Flowers of box-elder (apetalous and imperfect). A, pistillate; B, staminate.

Flowers with petals distinct from each other, as in St. John's-wort, are called *polypetalous.* Those like the morning glory, with united petals, are *gamopetalous* or *sympetalous.* Some like the box-elder, castor-oil plant, and buckwheat have no petals at all or only rudimentary ones. They are *apetalous.*

Flowers with petals all alike, such as the lily, apple, and rose, are *regular.* Those with differently shaped petals, like the pea, fox-glove, larkspur, and orchid, are *irregular.*

Most flowers have both stamens and pistils, and these are called *perfect,* in contrast with *imperfect* flowers that have either stamens or

FIG. 113. Cell from petal of St. John's-wort. Here the yellow color is due to the presence of chromoplasts.

pistils but not both. Examples of these are found in corn, squash, box-elder, and willow. They are of two kinds, *staminate* or *male,* and *pistillate* or *female.* If both staminate and pistillate flowers are on the same plant but distinct from each other, as in corn and squash, the species is called *monoecious;* if on separate plants, as in willow and box-elder, it is *dioecious.* We speak of monoecious and dioecious *plants* but do not apply these terms to the flowers.

Flower Colors.—Simple observation shows that the conspicuous color in flowers is usually localized in the petals, although the sepals may be colored also, as in fuchsia and larkspur. Microscopic examination reveals the position of the coloring matter in the cells. If flowers are white it is because of large and numerous intercellular spaces that refract the light. The yellow and orange pigments are in *chromoplasts.* The other pigments, notably the reds and blues, are usually dissolved in the sap of the central vacuoles. Not all chromoplasts, however, are yellow. Those of some fruits, including tomato and pepper, are red.

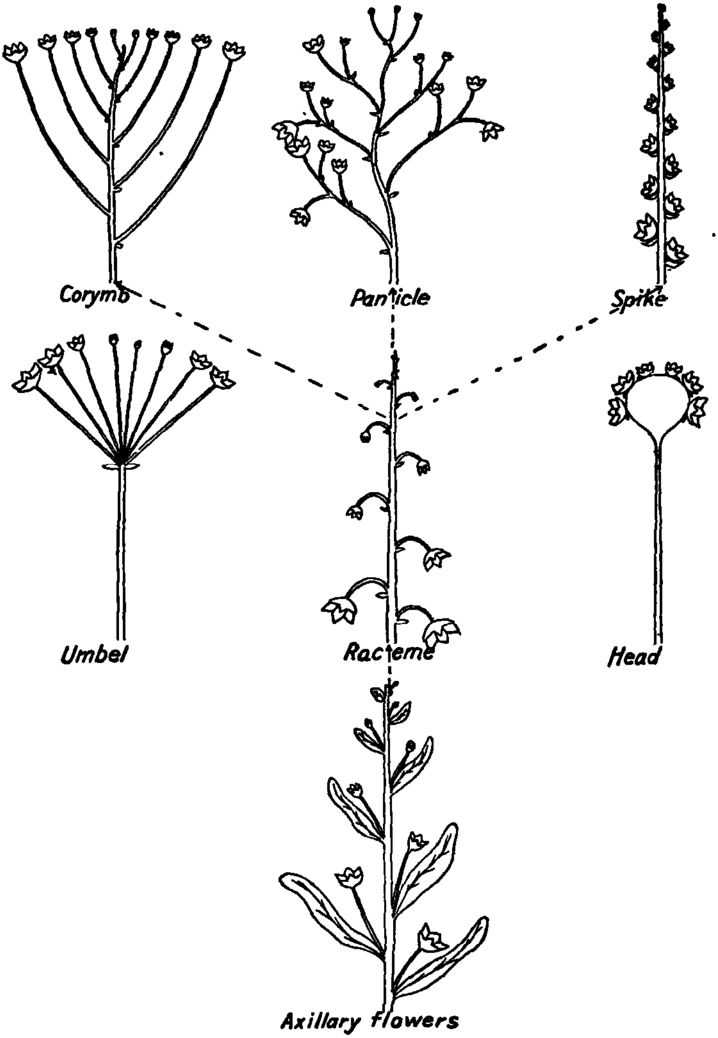


FIG. 114. Diagrams of inflorescences showing how one kind may be derived from another.

INFLORESCENCES

Some plants are showy because of their large individual flowers, others because of their flower clusters. These natural flower clusters are called *inflorescenses.* There are several kinds.

FIG. 115. Raceme of balloon mustard. The lower portion has already formed fruits while the upper portion has only buds.

The simplest and commonest inflorescence is the *raceme.* In it there is a central stem or *rachis* with the flowers attached along the sides by little individual stalks or *pedicels.* The lowest flowers open first while those at the top are only buds. Larkspur, lupine, currant, and chokecherry are good examples. The so-called heads of clover are racemes with a very short rachis that brings the flowers close together, suggesting a head.

If the rachis is rather short and the pedicels of the lower flowers are much longer than those of the upper so that the inflorescence is flat-topped we have a *corymb,* as in the hawthorn.

A *panicle* is virtually a branching or compound raceme. The lilac and grape illustrate panicles.

The inflorescences of the onion and the house geranium illustrate the *umbel.* In it all the pedicels are attached at approximately the same point at the top of the stem. The parsnip and many related plants have *compound* umbels in which the pedicels are attached to the tips of branches, which in turn are attached in clusters to the tip of the stem that bears the inflorescence.

Spikes differ from simple racemes in having sessile flowers, i.e., flowers without pedicels. However, the two kinds of inflorescence are intergrading. Plantains illustrate the spike.

The true head, like that found in sunflower and dandelion, resembles an extremely short spike. Its individual flowers are sessile and closely crowded on a disc-like expansion at the end of the stem.

Aments or *catkins* are like racemes or spikes but bear unisexual, apetalous flowers. They are illustrated by birch, alder, and poplar.

A rather rare inflorescence is the *cyme.* It is a loose, few-flowered inflorescence in which the terminal or central flower opens in advance

of those farther down. Cymes are mostly confined to plants with opposite leaves. They are found on the wild geranium, the greenhouse ice-plant, and St. John's-wort.

A highly specialized inflorescence is the *spadix*. It is a spike, the upper part of which bears staminate flowers and the lower part pistillate

FIG. 116. Spike of plantain. Like the raceme this is an indeterminate inflorescence, the lower flowers opening first.

flowers. Below this is a large enveloping leaf, the *spathe*, which is white or variously colored and grows up around the spadix. Two good examples are the calla-lily and the cat-tail.

Some plants have gone so far in the evolution of inflorescence as to make mixed or double types. Thus oats have panicles, but at the tip of each pedicel is a spikelet, not a single flower. The sage-brush of the West and most kinds of goldenrod have small heads arranged on the plant in the form of racemes, corymbs, or panicles.

FIG. 117. Aments (catkins) of poplar. The flowers are apetalous and unisexual. A, pistillate; B, staminate.

FIG. 118. Spadix of calla-lily. This is not a flower but an inflorescence. In the center is a spike, the upper portion of which bears staminate flowers and the lower portion pistillate flowers. The showy white portion is a spathe —a special leaf surrounding the spadix. Left, exterior view; right, with spathe removed to show spadix inside.

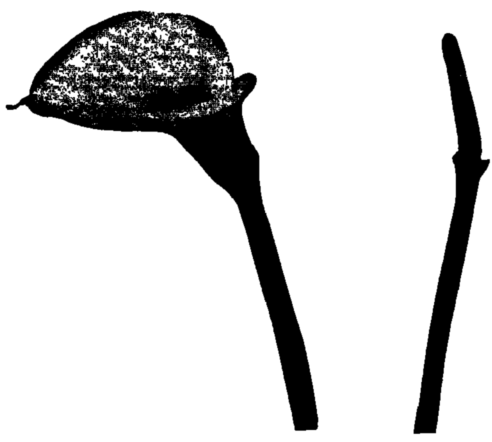


FIG. 119. Spadix of cat-tail. St, staminate flowers; P, pistillate flowers, S, spathe.

REVIEW QUESTIONS

1. Name the parts of a flower that take a *direct* part in reproduction.
2. Name the parts of a flower that do not take a direct part in reproduction.
3. Give the function of each part of a flower.
4. What is the distinction between "perfect" and "imperfect" flowers?
5. Which parts of a typical flower are specialized stem and which are specialized leaves?
6. Name five kinds of inflorescences.

7. What is the simplest kind of inflorescence?
8. How does it differ from a much-branched, flower-bearing top of a plant?
9. From the raceme how may the following be derived: (1) corymb, (2) spike, (3) panicle, (4) umbel, (5) head?
10. Describe a spadix.
11. What is a spathe?
12. How does a cyme differ from a corymb?
13. Why should not the white spathe of a calla-lily be considered a part of the flower?

CHAPTER XIII

POLLINATION OF FLOWERS

Flowers represent the highest development of reproductive organs in plants. It is their work to produce gametes of both sexes, bring them together, and from their union develop embryo plants in the seeds for the next generation. Since the pollen grains are spores that grow and produce male gametes, it is to the advantage of the plant that these

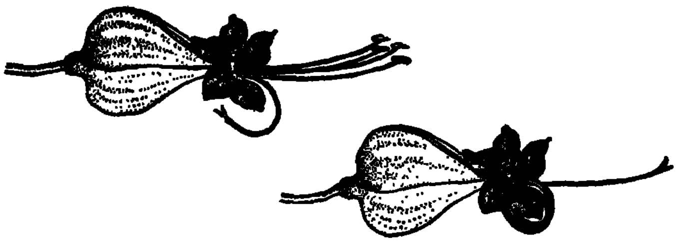


FIG. 120. Prevention of self-pollination in Clerodendron. Left, stamens ready to shed their pollen while the stigma is hidden under the petals. Right, stamens coiled under the petals while the stigma is exposed to pollen from other flowers. (Reprinted by permission from Brown's *The Plant Kingdom*, Ginn & Co.)

gametes be produced where they are in close proximity to the egg cells, or where they will be carried there by other agencies, as they have no power of locomotion. After the pollen has been formed, the next step in reproduction is its transfer to the stigma at the top of the pistil.

Self- versus Cross-Pollination.—In certain plants, for example pea, tomato, and some grasses, the anthers lie close to the stigma, and when they burst pollen comes directly in contact with it. Thus each flower pollinates itself. In other plants, such as corn, the pollen from the anthers of one flower may fall on the stigmas of other flowers of the same plant. The term *self-pollination* applies to both of these cases. In *cross-pollination* the pollen is transferred from the flower that produced it to the stigma of another on a different plant. There are several

devices that tend to prevent self-pollination and bring about cross-pollination, suggesting the likelihood that for some species, at least, it is the more desirable method. (1) In the flowers of some plants, such as the sunflower, red clover, and common plantain, the pollen grains ripen and the stigmas become receptive in any given flower at slightly different times. (2) In others the shape of the flower is such that self-pollination is unlikely to occur, or staminate and pistillate flowers are on

FIG. 121. Prevention of self-pollination in plantain. A, pistil mature and pollinated before stamens appear. B, pistil withered, stamens mature. (Reprinted by permission from Brown's *The Plant Kingdom*, Ginn & Co.)

different plants as is the case with box-elder and willow. (3) Some flowers, notably those of orchids, have become elaborately adapted to facilitate various methods of cross-pollination. In some varieties of cherry, pear, and apple close pollination is ineffective in producing fruit even though it takes place, pollen from a different variety being required.

Pollination by Insects.—We no longer suppose that the magnificence of flowers was designed for the esthetic pleasure of man. There is little doubt that their chief function, beyond the development of gametes, is to attract insects. This pre-supposes that the insects will be useful to the plant, for plants are no more philanthropic than other forms of life. A wholly unconscious co-operation has come about between certain insects and certain plants. The flowers, by their display of color and by their fragrance, attract the insects, which on their arrival obtain nectar and sometimes pollen for food. Carbonaceous food, chiefly used as a source of energy, is furnished by the nectar, and nitrogenous food

for the growth of the larvae is obtained from the pollen. Without intending to do so, these insects incidentally carry some pollen to the stigmas of other flowers.

Whole books have been written on the remarkable devices that have been evolved, some by flowers and others by insects, to perfect this co-operation and on the methods by which it is carried on. Indeed, most of the irregularities found in flowers, notably the orchids, are aids to

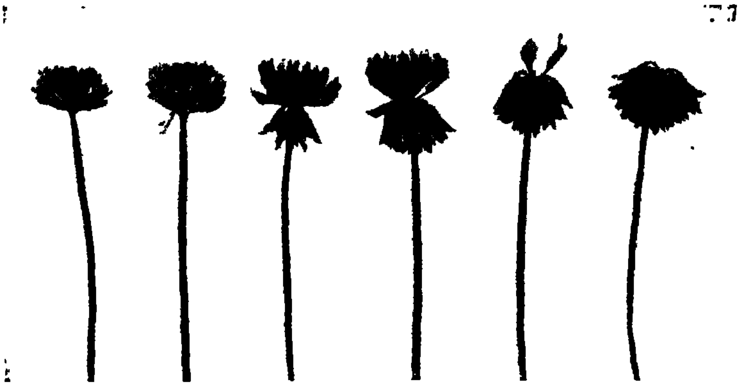


FIG. 122. Heads of white clover in stages of pollination. The erect flowers have not yet been pollinated.

the work of insects. The heads of white clover produce erect flowers. When one of these has been visited by a honey bee it droops, thus saving other bees from wasting their time in futile visits and increasing the likelihood that other flowers in the head will be pollinated in the same way. In alfalfa the staminal filaments form a sheath around the pistil. When the flower opens the pistil and stamens are held down in a strained position within the keel petals. However, the weight of a bumble bee or the insertion of its proboscis between the margins of the keel petals will "trip" the sheath of stamens so that they snap upward against the body of the insect, rupturing the anthers and scattering the pollen grains. Often, the stigma escapes pollination by these pollen grains and becomes cross-pollinated by a bee from another flower. If the flowers are not tripped by insects they may later trip of their own accord and self-pollination result. These are but two of the simplest illustrations of specialized insect pollination.

Among the more highly developed methods of insect pollination is that of the *Yucca,* or Spanish bayonet, of the arid West. The beautiful, pale-yellow flowers grow in large panicles and are dependent on a single species of insect for pollination. This insect is a white moth about a half-inch long. As egg-laying time approaches, the female yucca moth rests quietly until nightfall and then scrambles about the flowers of a cluster, or even visits nearby clusters, collecting a ball of sticky pollen. When this has been done she thrusts her ovipositor through a wall of the ovary of a flower and deposits eggs in several of the ovules. She then places her ball of pollen in the cup-shaped stigma of the same pistil. The pollen develops and fertilizes the ovules, some of which are destroyed by the developing larvae of the moth while others, not thus parasitized, develop seeds.

A B

FIG. 123. Pollination of *Yucca* flower. A, the Pronuba moth which pollinates the flowers; B, moth placing a ball of pollen on the stigma. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc. A, after Ganong; B, after Kerner.)

Still more remarkable is the pollination of the Smyrna fig. Here the reproduction of the plant is dependent upon a tiny wasp, which in turn cannot rear its young without the fig. The fig as we know it is a hollow inflorescence, the fleshy portion serving as a common receptacle for many flowers that develop inside it. This species is dioecious, some trees bearing figs with pistillate flowers that produce the fruit of commerce, while others bear mixed inflorescences containing staminate flowers along with a few pistillate flowers that do not produce seed. No figs develop on these trees.

The female fig wasps hatch from eggs laid in the ovaries of these sterile pistillate flowers and wander about the interior of the mixed inflorescence until they are coated with pollen grains. Then they change their tactics, and, leaving their homes, fly to other fig trees seeking new inflorescences. To reproduce they must find mixed inflorescences, for here the pistillate flowers have short styles which permit them to lay eggs in the ovaries where their young develop. Some of the wasps,

however, by mistake enter pistillate inflorescences. This is their misfortune, for they cannot escape because of the sharp scales in the orifice, neither can they lay their eggs in the ovaries of the flowers because the styles are too long for their ovipositors. In their struggles they pollinate the flowers and then die without reproducing.

It is a matter of history that the early inhabitants of Smyrna planted the "wild," or "male," figs near their fruit-bearing fig trees, or gathered

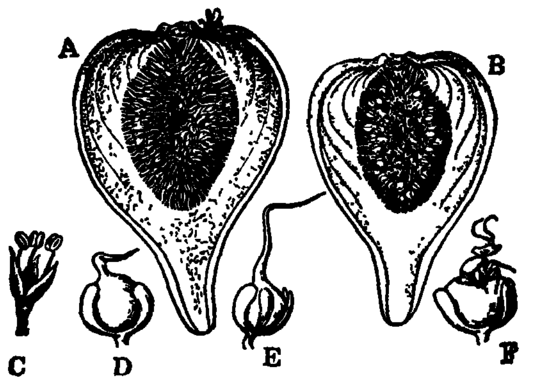


FIG. 124. Pollination of the fig A, longitudinal section of pistillate inflorescence, which produces the fig of commerce; B, longitudinal section of mixed inflorescence, which produces no fig; C, staminate flower from B; D, short-styled pistillate flower from B; E, long-styled pistillate flower from A; F, fig wasp emerging from pistillate flower in B. (From Mottier's *Textbook of Botany*, P. Blakiston's Son & Co. After Kerner.)

branches of the staminate forms and hung them in their cultivated trees, knowing the benefits thus obtained but not understanding the reasons. When the Smyrna fig was introduced into California it failed to produce fruit, even with the staminate trees present, until the fig wasp was imported and became established in the trees.

Not all insect-pollinated flowers are of special construction. Of the species pollinated in this way great numbers have flowers that are entirely regular and without special devices for applying pollen to the bodies of insects or removing it from them. The apple flower is an example. Bees visit even the apetalous willow.

Pollination by Wind.—Wind-pollinated flowers have very dry, light pollen that remains suspended in the air for some time and may be carried a considerable distance. This is an extremely wasteful method,

for most of the pollen fails to light on a suitable stigma and is lost. It is most effective in monoecious plants such as corn and elm, or in dioecious plants like poplar and willow when closely crowded.

Wind-pollinated flowers, such as those of oak, poplar, and many grasses, are usually apetalous and without fragrance. Often the stamens and pistils protrude far beyond the other floral parts and the stigmas are large and feathery. The pollen is dry and usually abundant. The anthers of nettle and some other species explode and throw the pollen into the air. Some flowers are not restricted to one method of pollination. If not visited by insects soon after opening they discharge their pollen into the air. These cases suggest the possibility that since the floral types were developed as adaptations to wind or insect pollination conditions have changed, and a different method of pollination has been adopted; but the floral structure in these species has remained essentially the same.

Other Methods of Pollination.—A large number of species, especially in the tropics, are pollinated by humming birds; the pollen of some aquatic plants is carried into the flowers by currents of water; but wind and insects are by far the most important agents.

Theoretically, only as many pollen grains would need to reach the stigma as there are ovules in the ovary. Actually, however, many times more are produced than ever find such a lodgment and vast numbers are lost, especially in wind-pollinated species. Excessive production of pollen is, however, much less disastrous than the failure of flowers to produce seed for want of pollination.

Conservation of Pollen.—Pollen is so essential to the perpetuation of flowering plants that unnecessary waste must be reduced to a minimum. Much loss of pollen is inevitable in any method of pollination, but some interesting devices have been evolved that help to protect it.

When plants maintain a supply of material as desirable as nectar, it is inevitable that insects that cannot aid in cross-pollination will help themselves along with the others. Ants do not travel as widely as flying insects, and many kinds of insects are so small that they enter the flowers, partake of the nectar, and withdraw again without carrying pollen. In some cases such insects are kept out by hairs in the flowers or by sticky glands on the stems, illustrated by the Nottingham catchfly and twin-flower. In some of the balsams nectar is produced by the leaf stipules in such a quantity that ants visit them in preference to the flowers.

The wetting of ripe pollen grains in the anthers by rain or dew makes them less easy of distribution and may cause them to deteriorate. In a considerable number of species the pollen is sheltered from rain. Many bell-shaped flowers are pendant, with the opening downward. In a species of *Campanula* the flowers are erect when exposed to sunshine

FIG. 125. Protection of pollen from rain. 1. *Ariopsis peltata,* the flowers in a spadix with spathe above it. 2. Globe-flower, with perianth covering the stamens. 3. *Digitalis lutescens,* with corolla tube turning downward, thus shedding the rain. (After Kerner.)

but pendant in cloudy weather and at night. In a few species the flower, borne in the axil of the leaf, swings down underneath the leaf by the bending of the peduncle and in this way obtains shelter. The ray flowers of the Carline thistle, which has a daisy-like head, lie flat in strong light but bend upward as the sun becomes overcast or sets, thus covering the central flowers of the head with a conical roof. In some crocuses a similar effect is produced by an upward bending of the perianth, temporarily closing the flower. The perianth of the Globe-flower of the arctics never fully opens and thus provides a permanent covering, pollination being effected by insects that enter by crawling between the loosely folded sepals and petals. The spathe may surround

the spadix in such a way as to protect it. This is strikingly true of a Japanese species of *Arisema* in which it forms an "umbrella" over the spadix, which lies in a horizontal position beneath it.

Flowers that normally are self-pollinated have many devices for getting pollen to the stigmas without the aid of wind or insects. These include movement of the anthers close to and above the stigmas by bending of the filaments, bringing the two close together by movement of the petals, and explosion of the anthers.

Review Questions

1. What is meant by self-pollination?
2. State two methods by which it is prevented
3. Name the two chief agencies for cross-pollination, and three of lesser importance
4. State in a general way how insect-pollinated flowers differ in morphology from wind pollinated flowers?
5. Why do insects visit flowers?
6. Name two advantages of insect pollination over wind pollination
7. Name and describe an especially complicated case of insect pollination.
8. Under what conditions could the insect method of pollination be a disadvantage to a plant?
9. What determines the number of pollen grains that a flower receiving them can use to advantage?
10. What advantage is served by having more pollen grains produced than there are ovules?
11. Under what conditions might so high a specialization in method of pollination as that found in *Yucca* or the fig be a detriment to the plant?
12. Since close pollination is the most economical of pollen of any, why would any other method have been evolved?
13. How do some plants prevent crawling insects from stealing their pollen?
14. Give five ways by which anthers are protected from rain.

CHAPTER XIV

PRODUCTION OF SEEDS AND FRUITS

The chief method of reproduction in flowering plants is the formation of seeds enclosed in fruits. To comprehend the processes involved it must be realized at the start (1) that the ovary develops into the fruit, (2) that each ovule develops into a seed, (3) that an ovule will not develop unless its egg-cell is fertilized by a male nucleus from a pollen tube, and (4) that the ovary may or may not develop if all or part of the ovules remain unfertilized.

Growth of the Pollen Tubes.— Some kinds of pollen grains will germinate in pure water but others will not. As a rule the stigma is rough and secretes a moist, viscid material in which germination is reasonably certain.

When a pollen grain germinates it absorbs moisture, thus increasing the turgor of its contents. The wall softens slightly, in many species at a special *germ pore* where it is thin, and a germ tube is pushed out at that point.

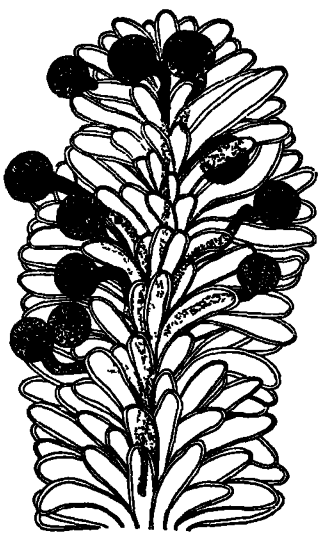


FIG. 126. Pollen grains germinating on the stigma of purslane. (From Brown's *Textbook of General Botany*, Ginn & Co.)

The germ tubes from the pollen grains push directly into the stigma. They force themselves through the intercellular spaces of the stigma and style, pushing the cells aside or even crushing them. Utimately they reach one or more cavities in the interior of the ovary where the ovules are produced. In some plants the ovules fill the chambers, in others there is more or less air space around them. Each ovule has a natural opening, or *micropyle,* through

which the pollen tube enters. Through some unknown influence the tips of the pollen tubes are guided to the ovules. The one that first

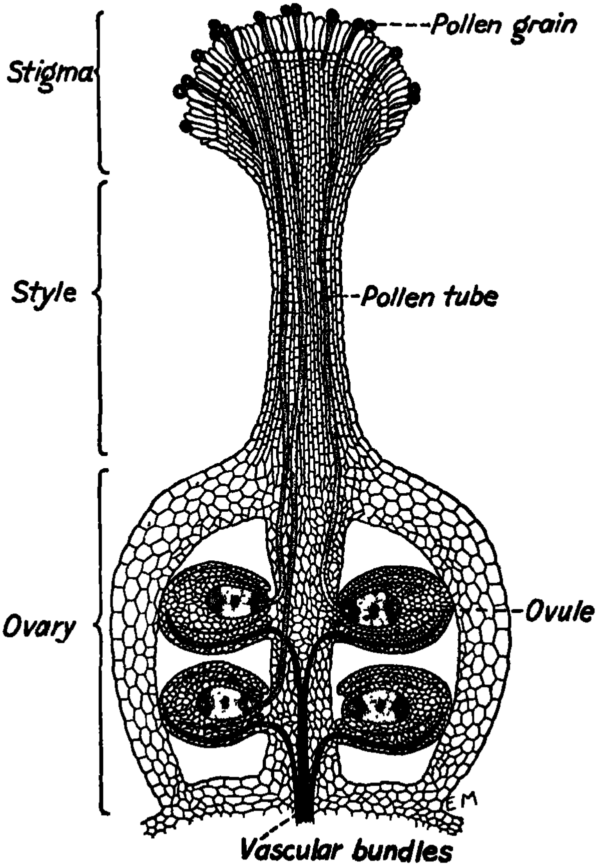


FIG. 127. Longitudinal section of flower pistil, showing pollen tubes growing through the style and entering the ovules. Diagrammatic.

reaches a micropyle enters it and discharges a gamete nucleus into the egg cell. If the ovary contains more than one ovule, as is usually the case, the eggs in the others are similarly fertilized by sperm nuclei from other pollen tubes. Any ovules that are not found by pollen tubes and

any pollen tubes that are too late to find unfertilized ovules soon wither and die

As will be explained in detail later (page 359), the pollen grain is not a male gamete In its germination and production of a pollen tube nuclear division takes place, resulting in several nuclei—usually three Two of these are capable of functioning as gamete nuclei, and one of them normally unites with the egg nucleus in the ovule

Development of the Seed.—With the fusion of male and female nuclei the formation of the *embryo* begins This is the young plant of the next generation The fertilized egg cell divides, the two daughter cells divide, and the process continues until a considerable number of cells have been formed, all pretty much alike. Cell division continues and the cells begin to differentiate into the organs of the embryo In the bean, a dicotyledonous plant, the most conspicuous part of the embryo is two fleshy seed leaves, the *cotyledons,* in which food is stored These are attached to a tiny stem The portion of the stem above the cotyledons (when the seed germinates) is the *epicotyl,* which has a bud, the *plumule,* at its tip The portion below the cotyledons is the *hypocotyl* This connects the cotyledons with the *radicle,* or rudimentary root The embryo of corn has only one cotyledon, which stores but little food, for most of the food storage is in the *endosperm,* which is a structure outside the embryo but developed along with it (See page 371)

The embryo as it develops is enclosed within the *nucellus,* which is the body of the ovule One might suppose that this would form a seed coat around the embryo, but it does not develop and thicken and as the seed matures it is largely absorbed There are one or two *integuments* that originate near the base of the ovule and develop progressively over it except for a tiny opening, the micropyle, which remains more or less open These integuments are the seed coats

Development of the Fruit.—As the ovules grow into seeds the walls of the ovary enlarge and thicken to form the fruit Usually the style and stigma wither as soon as fertilization has been accomplished Strictly speaking, the fruit is formed from the ovary only, but in some cases accessory organs develop along with it Thus, in the apple the calyx persists in the blossom end, and the receptacle develops into the fleshy portion In the blackberry there are many pistils on a common receptacle which remains inside when the fruit is picked. In the strawberry this receptacle develops into the edible pulp while the numerous fruits on the surface are hard and seed-like.

Kinds of Fruits.—It is logical, from a botanical standpoint, to call the developed ovary a fruit, whether it is soft and juicy or hard and dry. An example will show the reason for this. The almond and the plum are very closely related. Their blossoms are almost identical and their seeds and fruits are likewise similar in their early development. The seed in both cases is covered by the inner ovary wall hardened

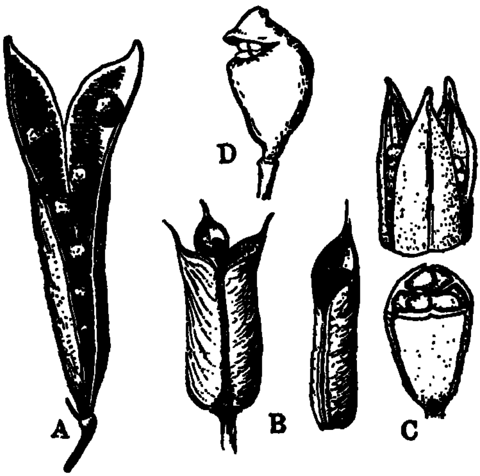


FIG. 128. Dry, dehiscent fruits. A, pod or legume of sweet pea; B, follicles of monkshood; C, capsule of *Iris;* D, capsule of *Jeffersonia.* (From Mottier's *Textbook of Botany,* P. Blakiston's Son & Co. After Faguet.)

into a "stone" or "pit." As they mature, however, the outer part of the ovary wall becomes juicy in the plum and tough and leathery in the almond. Morphologically they are the same structure. Since they have the same type of origin they are said to be *homologous* with each other.

We have, then, *fleshy* and *dry* fruits. A dry fruit from a pistil of one carpel is a *pod* or *legume.* A dry fruit of several carpels is a *capsule.* Flax, cotton, and poppy are examples.

If dry fruits open of their own accord to release the seeds, they are *dehiscent;* otherwise, they are *indehiscent.* Some of them dehisce explosively or with a snap, throwing the seeds for a distance of several feet.

Many dry fruits are small and contain only one seed. These are

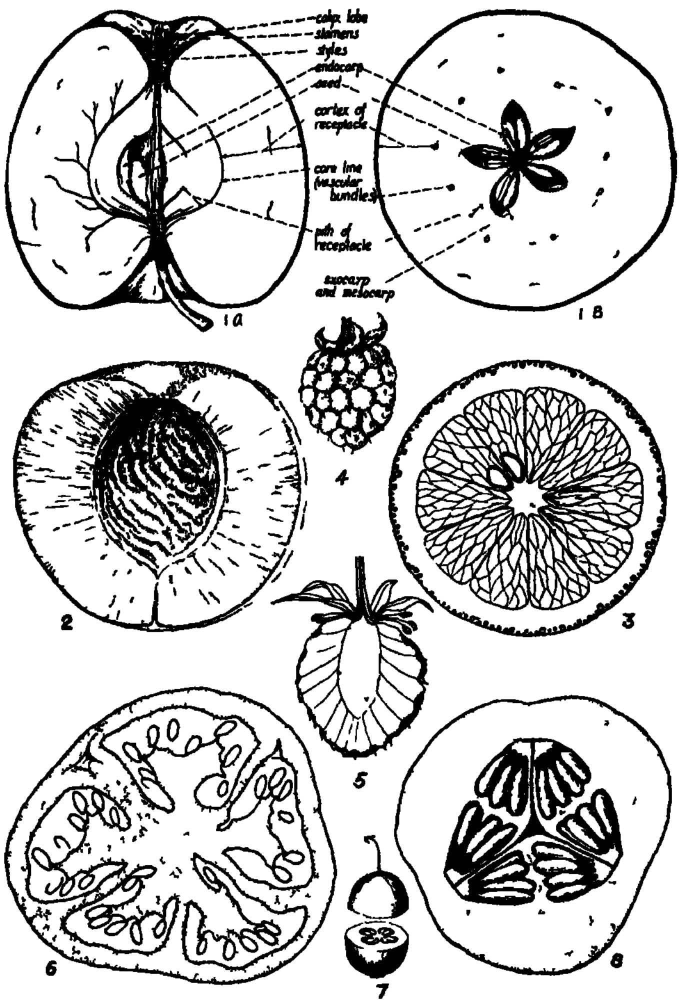


FIG 129 Kinds of fleshy fruits 1a and 1b, apple, illustrating pome (after Robbins), 2, peach, illustrating drupe (after Decaisne), 3, orange, illustrating berry (after Decaisne), 4, raspberry, illustrating aggregate fruit (after Chamberlain), 5, strawberry, illustrating aggregate fruit (after Brown), 6, tomato, illustrating berry (after Smith, Overton, et al), 7, cranberry, illustrating true berry (after Gray), 8, cucumber, illustrating pepo (after Chamberlain) (Redrawn)

achenes. The entire fruit resembles a seed and this term is commonly applied to it. The sunflower and dandelion are examples. Achenes not infrequently bear plumes or wings that aid in their distribution. These appendages may be developments of the style, but more often they come from the calyx. The dandelion and thistle have such plumes.

FIG. 130. Round-topped plants of tumbling mustard blown by the wind and scattering seeds.

The true *nut,* such as the filbert or acorn, is much like an achene but larger.

A dry fruit of great importance to man is the *caryopsis,* represented by wheat, corn, rice, and other grains. It resembles an achene in being a small, dry, seed-like fruit. Its one seed adheres tightly to the surrounding ovary wall, and contains a relatively small embryo and a very large endosperm.

Fleshy fruits are classified as *simple, aggregate,* and *multiple.* The *berry* is an example of a simple fruit. The botanist is logical in his restriction of the term berry to a fleshy fruit with several seed chambers and many seeds developed from a single pistil, as illustrated by the cranberry, huckleberry, and grape.

The blackberry, raspberry, and strawberry are very different in morphology from the true berry, being derived from many pistils in

one flower attached to a common receptacle They are *aggregate* fruits

The *multiple* fruit, illustrated by the mulberry and the fig, is a collection of ripened ovaries, each from a single flower in an inflorescence The entire inflorescence is required to produce one multiple fruit

A considerable number of special names are in use for fruits, such as *pome* (apple, pear, etc), *drupe* (peach, plum and cherry), and *pepo* (pumpkin gourd, etc)

Seed Dispersal.—Each plant may produce many seeds—often hundreds, sometimes thousands The author has estimated as many as a million on a large tumbling mustard The advantage of getting these seeds scattered far and wide is obvious, but how can it be done? For the most part they have no power of locomotion so they must depend on outside agencies Naming these in the order of their importance (aside from man), we have (1) wind, (2) animals (including birds), and (3) water By evolutionary processes different plants have perfected ways of making the best use of each of these carriers

Where there is no special adaptation of the plant for wind distribution of its seeds, fragments may be torn from it and blown about The simplest of the adaptations to wind distribution is a rounded top that is easily detached from the root and blown about as a 'tumble weed" Russian thistle and tumbling mustard are excellent examples Some achenes and other small, dry fruits borne on trees are provided with *wings* that give the seeds a spinning motion and thus delay the fall so that they may be carried several yards from the mother tree Well-known examples are elm, maple, box elder, and ash Still more effective are *plumes* Those of the dandelion and thistle are relatively large for the size of the achene and are exceedingly effective A few plants, notably cotton, fireweed, and one of the milkweeds, produce plumes on the seeds inside dehiscent capsules

More specialized devices are provided for distribution by animals The chief purpose served by highly colored and edible fruits is to attract animals and birds Some very tiny seeds are not swallowed but are carried on mouths or feet and are later rubbed off at some distance from the place of repast Others are swallowed, but, because of impervious seed coats, pass through the alimentary tract undigested Nuts are carried by squirrels and dropped in a moment of panic or are stored away and never called for

Particularly interesting to the naturalist, but annoying to the traveler, are various hooks and spines by which dry fruits cling to the clothing or to the fur of passing animals. These clinging fruits are

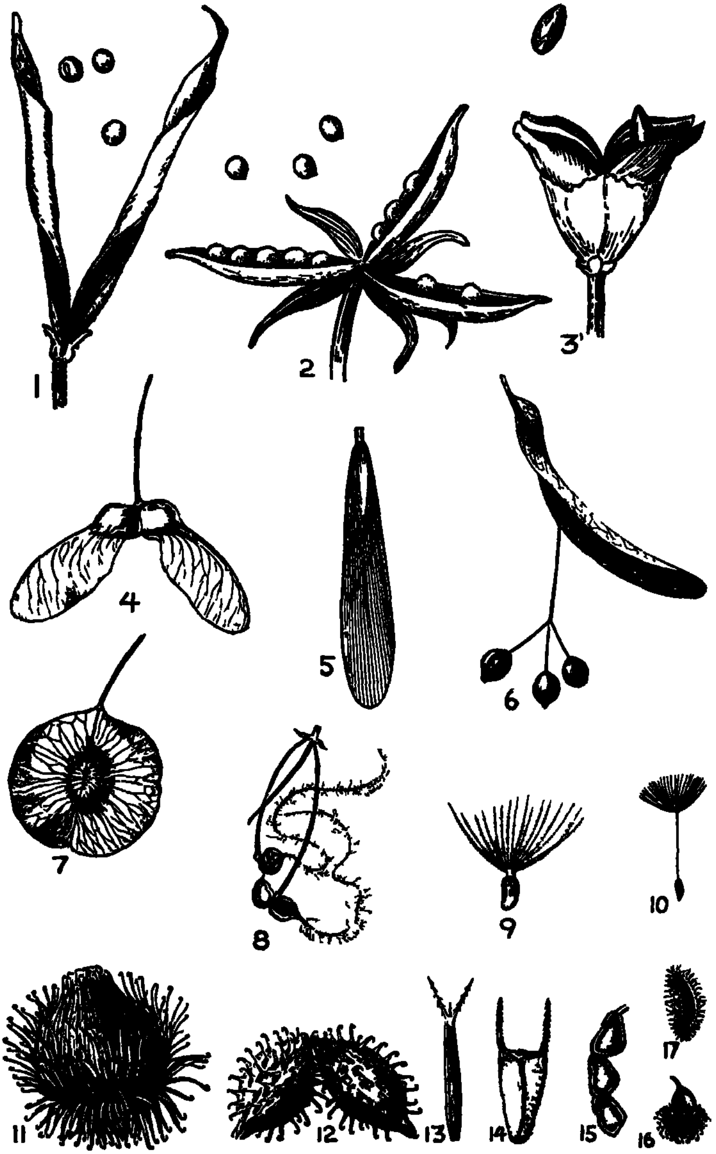


FIG. 131. Dry fruits with devices for dispersal of their seeds. One to three by sudden dehiscence: 1, wild bean; 2, violet; 3, witch hazel. Four to ten, by wind: 4, maple; 5, ash; 6, basswood; 7, elm; 8, *Clematis*; 9, thistle; 10, dandelion. Eleven to seventeen, by animals: 11, burdock; 12, cocklebur; 13, Spanish needle; 14, beggar's tick; 15, beggar's lice; 16, agrimony; 17, carrot. (Redrawn from various sources.)

given such uncomplimentary names as "beggar's lice," "ticks," etc. Burdock, cocklebur, two kinds of buffalo bur, sand-bur, and devil's pitchfork are other common names for these fruits and the plants that bear them.

Seed distribution by water is not so common but is sometimes very effective. Fragments or practically entire plants may be carried downstream for miles. The plumed fruits of cottonwood and willow are borne by streams as well as by wind. Particularly effective is the irrigation system of the West, in which most of the weeds growing on the banks of irrigation ditches become spread onto the land by water carrying the seeds.

Man himself has become a great distributor of weed seed through commercial practices. He alone is responsible for transporting seeds across the ocean, and many of the worst weed pests have been thus introduced into America from Europe as intruders in the seeds of grains, grasses, and other crop plants.

FIG. 132. Squirting cucumber. Pressure develops inside the fruit, and as it is detached a hole is torn through which the seeds are discharged with the juice. (From Mottier's ***Textbook of Botany***, P. Blakiston's Son & Co. After Jenkins.)

While wind, water, animals, and man are the chief carriers of seeds, there are a few plants that have developed the power of throwing their seeds for a short distance. The method is usually by the sudden dehiscence of a dry fruit such as a pod. As the fruit dries it shrinks unevenly, and this develops a considerable strain on some part, usually in the region where the opening is to appear. When the fruit opens it does so with a sudden violence that throws the seeds out, sometimes for several feet. The seeds of witch-hazel, for example, are scattered in this way. A different mechanism is found in the squirting cucumber. The cavity of this fruit, when ripe, is filled with a liquid containing the seeds. This liquid develops considerable internal pressure. Finally, when the fruit loosens and drops from its stem a hole is torn through

the wall at the place of attachment, and the liquid is squirted out, carrying the seeds with it In this discharge there is some recoil that may give the fruit an end-over-end motion in its fall.

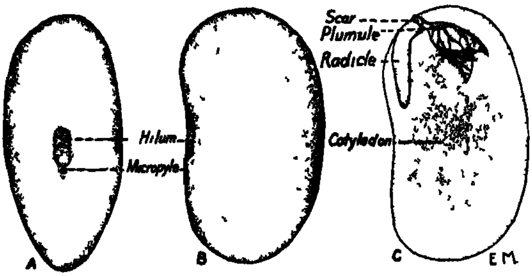


FIG. 133. Bean seed, soaked and ready for germination A, edge view; B, flat view, C, with seed-coat and one cotyledon removed.

Seed Germination.—A seed must be looked upon as a tiny embryonic plant of the new generation, with enough stored food to start it off in life and seed coats for protection. After maturity, seeds lie dor-

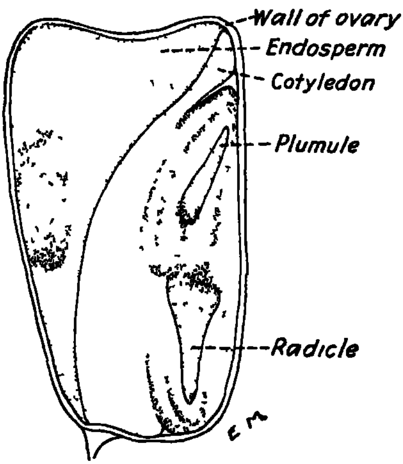


FIG. 134 Longitudinal section through grain of corn.

mant until conditions are suitable for growth. Some are capable of germination when first formed, but others require a rest period of a few months. The length of time that seeds will remain viable varies

with the species and also with storage conditions. The maximum period for most species varies from two to ten years. Geranium seeds, however, have been germinated when more than fifty years old. Seeds of the

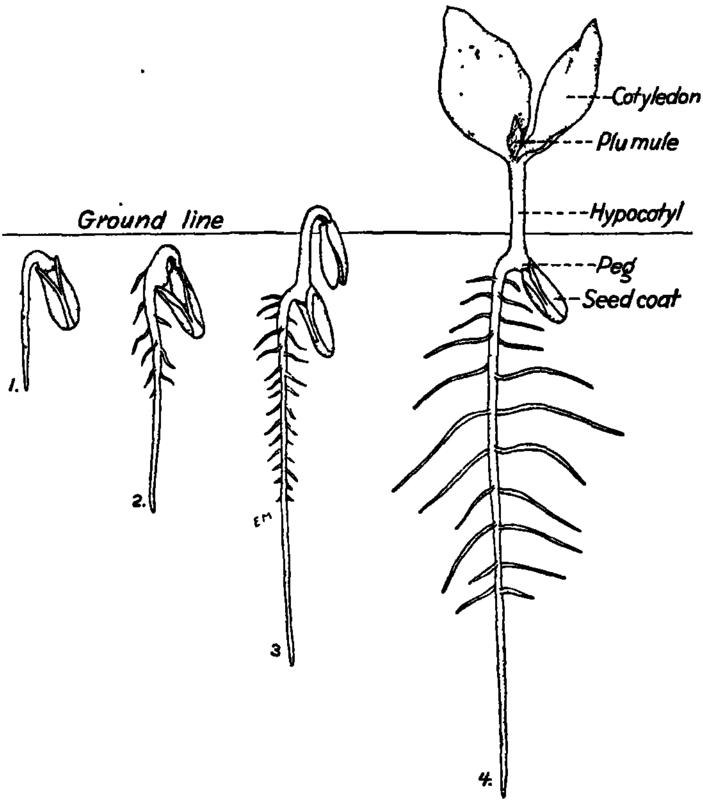


FIG. 135. Seed germination in the squash. As the embryo develops a "peg" or "heel" is formed that holds the seed-coat while the cotyledons are pulled out of it.

Indian lotus, recovered from peat in an old lake bed in Manchuria, proved capable of germination. The peat containing the seeds was estimated to be between 150 and 200 years old. Reports of viable seeds having been found in the ancient tombs of Egypt and in the remains of cities buried by volcanoes centuries ago are without verification. In

some cases seeds that were claimed to be from ancient ruins have germinated into plants of varieties only recently produced. Delicate experiments have indicated that a very slight amount of carbon dioxide is being evolved by dormant seeds, and this could not go on for centuries without consuming the available food supply. Most seeds escape from their fruits before germinating, but achenes and nuts remain covered by the ovary wall. Occasionally seeds germinate inside fleshy fruits such as apples and oranges.

The conditions for seed germination are suitable temperature, moisture, aeration, and, for most species, absence of light. The seed-coats take up moisture by imbibition, and some of this moisture is transferred to the embryo and endosperm, causing the entire seed to swell. Finally the seed-coat bursts, and the embryo sends its first root down into the soil and its stem bearing the plumule up into the air. Elongation of the epicotyl pushes the plumule upward. If the hypocotyl elongates also, the cotyledons are pushed up above the surface of the ground, as in the bean, sunflower, and squash. If the hypocotyl does not elongate, the cotyledons remain below ground, as they do in corn and other monocotyledons and in the pea.

The pumpkin and its relatives have an interesting method for freeing the cotyledons from the seed-coat. The middle of the bent hypocotyl emerges first and a "heel" or "peg" at its base remains attached to the edge of the ruptured seed-coat. As the hypocotyl elongates it forces the cotyledons out, the seed-coat being held back by the peg to which it is attached.

Review Questions

1. What does each of the following flower parts develop into: (1) peduncle, (2) ovary, (3) ovule, (4) ovule wall, (5) fertilized egg?
2. Describe the surface of a stigma.
3. Describe the behavior of a pollen grain following pollination.
4. What is the distinction between pollination and fertilization?
5. Why is it illogical from a botanical standpoint to call both cranberries and raspberries berries?
6. Define: (1) micropyle, (2) drupe, (3) capsule, (4) endosperm, (5) dehiscent, (6) aggregate fruit.
7. Why should an achene be classed as a fruit rather than a seed?
8. Name the two chief agencies by which seeds are distributed and three others.
9. Which agency carries seeds the longest distance? Illustrate.
10. What conditions are most generally favorable to seed germination?
11. By what process does moisture pass through the seed coats?

12. Name the parts of a young bean or squash seedling.
13. Name three kinds of plants in which the cotyledons appear above ground and two in which they do not.
14. Explain how it happens that there is often a natural opening through the seed-coats.
15. Point out two errors in the following statement. "In beggar's ticks the seed is provided with tiny hooks in order that they may catch in the hair of passing animals and thus be carried about."

CHAPTER XV

VEGETATIVE PROPAGATION

In all higher plants and in most lower ones we recognize two portions, the plant body, or vegetative portion, and the structures that aid in reproduction. Nearly all higher plants reproduce by seeds, but some of them are also propagated, either naturally or artificially, by vegetative parts. While it is difficult to get new pine trees, for example, or new plants of most annual species from anything but seeds, it is common knowledge that house geraniums, strawberries, and potatoes are regularly propagated without seed.

Natural Vegetative Propagation

A number of structures have been evolved for increasing plants vegetatively without the aid of man.

FIG. 136. Strawberry plant propagating by runners.

Runners or Stolons.—The tips of stems coming in contact with the earth sometimes take root and then develop new plants. When these are well established there is a tendency for the newly formed plant to become severed from the parent, partly by death of the connecting portion and partly by the action of wind, etc. Such specialized stems are

called *stolons* or *runners*. In the black raspberry, or blackcap, they are ordinary-looking canes, but in the strawberry they are almost leafless and serve no other purpose. This method of propagation is not a com-

FIG. 137. Walking fern. The leaf tips send adventitious roots into the soil and adventitious shoots bearing leaves into the air, thus forming new plants. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

mon one, and yet a considerable number of examples could be added to those already mentioned.

In the walking fern the leaves function in the same way as stolons. Their tips come in contact with the ground and produce adventitious roots and stems, thus starting new plants.

Underground Stems or Rootstocks.—Instead of extending above ground as stolons, stems may push their way horizontally underground. The thinking student may challenge the identity of these structures as stems, questioning whether they are not roots. However, the nodes and scale-like leaves which they bear show them to be stems. Adventitious roots grow out from the nodes, and stems are sent up to the surface of

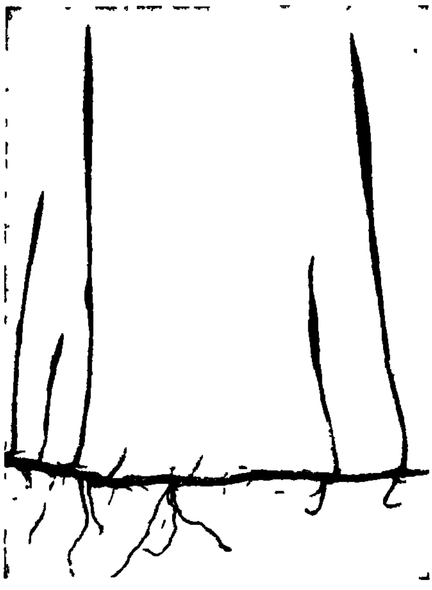


FIG. 138. Rootstock of quack grass. This slender underground stem grows *rapidly and sends shoots up into the air and adventitious roots into the soil*

the ground and into the air at some distance from the original plant. These *rootstocks,* or *rhizomes,* are produced by several species of grasses, e.g., quitch grass, couch grass or quack grass, by Solomon's seal, by peppermint, and by a number of other species.

Tubers.—A true tuber is a fleshy underground stem, often connected with the mother plant by a slender rhizome. There is no better example than the common white potato. Each "eye" of the potato is a bud or a collection of buds in the axil of a tiny scale-like leaf and is capable of developing a stem and adventitious roots. These leaf scales are most easily seen on young tubers, those not more than half grown. After they have matured and been harvested they are not so conspicu-

ous. Most tubers lie dormant until the season following the death of the mother plant and hence must contain a good supply of stored food.

Bulbs and Corms.—*Bulbs* are commonly produced by monocotyledonous plants such as lilies, hyacinths, tulips, and onions. Each bulb consists of a very short stem, bearing the thickened bases of leaves which serve for the storage of food. In structure it is like a huge bud. *Corms* are similar in shape, but consist almost entirely of short, thick, leafless stems. They are found in the gladiolus, crocus, and some grasses. Bulbs and corms are generally produced underground in considerable numbers and are very effective reproductive bodies. If they accidentally become scattered the plant is fortunate, for it has no special method for their distribution.

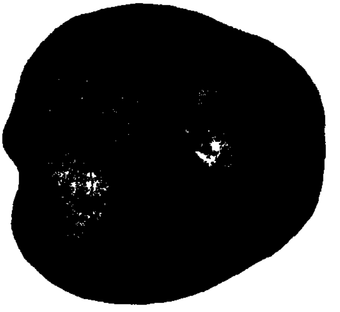


FIG. 139. Potato tuber with scale-like leaf at the "eye," which contains several buds.

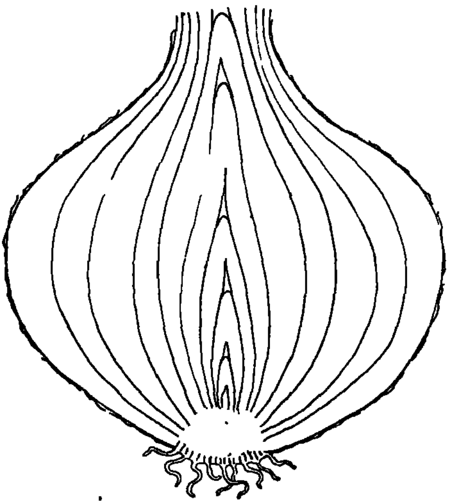


FIG. 140. Onion bulb composed of the scale-like, fleshy bases of leaves attached to a short, thick stem.

Special Underground Roots.—Usually roots serve only to support the stems that grow from them and take no direct part in propagation,

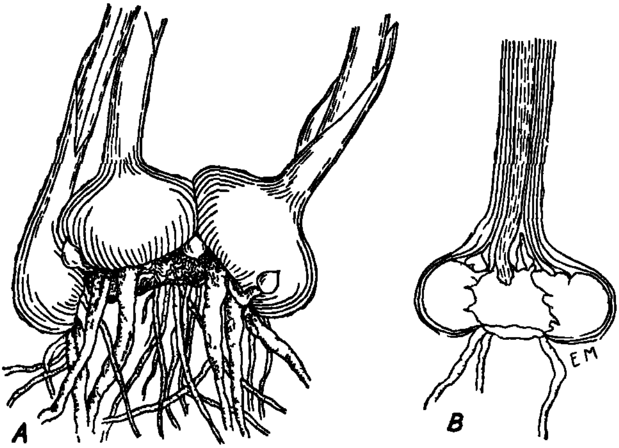


FIG. 141. Corms of *Gladiolus*, consisting chiefly of fleshy stems. A, external view; B, internal view.

FIG. 142. Fleshy fascicled roots of *Dahlia*.

but there are some exceptions. The small-flowered, wild morning-glory is a perennial that produces great numbers of long wiry roots, which extend laterally and send up adventitious stems at frequent intervals.

Thus large patches of morning-glories are produced, and if by any means the ground is broken and the fragments scattered, the plants are dispersed.

Single fleshy roots do not serve as a means of propagation, but fascicled fleshy roots increase the number of individuals in the same way as do tubers, bulbs, and corms. Familiar examples are the dahlia and sweet potato.

Artificial Vegetative Propagation

Civilized man has taken advantage of the tendency of plants to *regenerate* lost parts, that is, their tendency to build new parts that take

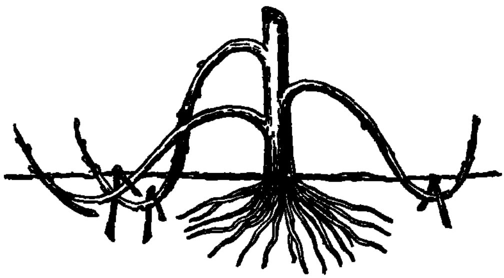


Fig. 143. Method of layering. (From Gager's *General Botany*, P. Blakiston's Son & Co.)

the place of those lost. This may occur in nature as a result of accident, but man has developed the tendency into very important methods of propagation.

Layering.—Our grandmothers propagated a number of woody perennials—roses, lilacs, and currants—by layering. Some of the lower branches were bent to the ground, covered with earth, and weighted down. Often the covered portion was wounded to induce the formation of adventitious roots. After waiting a time for roots to start from the covered portion, the branch connecting it with the old plant was severed, and the new plant was placed on its own resources. This method is cumbersome and rarely used on a commercial scale, but it succeeds with some shrubs that do not grow readily from cuttings, the advantage being that the layered portion is nourished for a time by the mother plant.

Cuttings.—Cuttings differ from layers in that the pieces of stem are removed and planted without previous rooting. "Hardwood" cuttings made from young stems in the dormant condition are extensively used by nurserymen for a considerable number of trees and shrubs, including willows, poplars, lilacs, and currants. Some of these woody plants are rarely propagated by any other method.

Many herbaceous plants also are propagated by cuttings, using pieces of stems in an actively growing condition. Geraniums, wandering Jew, and other small plants are propagated in this way for greenhouse use. Sugar-cane is propagated commercially on a large scale by stem cuttings; pineapples, by cuttings from fruits and by pieces of stems that include large lateral buds.

Cuttings, to succeed, are obliged to regenerate their roots. The tendency is for these to grow from the lowest buried node, but some plants regenerate freely from the cambium layer at the cut end and others from internodes. In root cuttings, which are used to propagate a few species, the new stem starts from an adventitious bud usually originating in the pericycle.

Very few plants can be propagated by leaves, but the *Bryophyllum* of greenhouses produces in the notches of its leaves tiny, rudimentary plants that develop readily if the leaves are removed and partly buried in wet sand. Some begonias also can be propagated from leaves.

Grafting and Budding.—The process of grafting a piece of a plant onto another plant has long been known. It is more or less applicable to most dicotyledonous plants and is extensively used with a few, especially fruit trees. In the apple, for example, if a piece is cut from the dormant growth of the previous season and kept moist and cool, the cambium layer at the cut end will set up a special activity and form a rather soft growth called a *callus*. Suppose that a freshly cut end is fitted into a suitable incision in another plant and each forms a callus on the injured surface. The two calluses will press against each other and the two pieces will grow together. This is the fundamental principle underlying grafting. The term *stock* and *scion* have been applied respectively to the plant receiving the piece and the piece that is grafted into it. There are three important details that are essential to success in grafting: (1) The cambium layers of stock and scion must be in contact in one place at least—the more the better. (2) Stock and scion must be pressed firmly together. (3) The wounded surfaces must not be allowed to become dry before the calluses have time to form. Vari-

ous kinds of joints are in use for fitting the two pieces together. Stock and scion do not have to be of the same species or even be closely related, although some plants are more easily grafted than others.

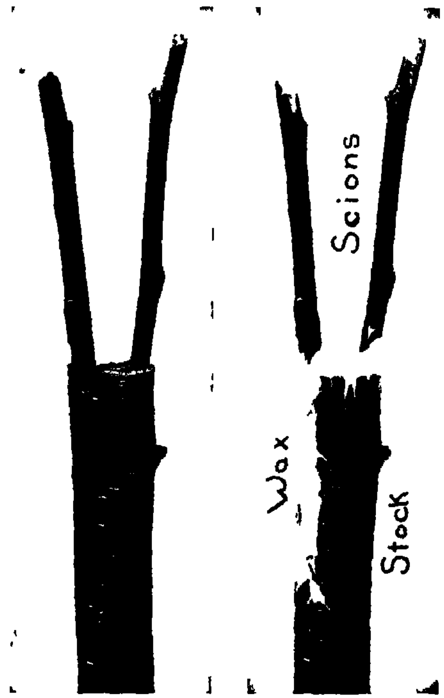


FIG. 144. One method of grafting—cleft grafting. The scion (above) and the stock (below) are joined in such a way that a portion of the cambium layer of the one is brought into close contact with a portion of the cambium layer of the other. The wound is then protected by grafting wax.

Budding is much the same in principle as grafting. In one of the commonest methods a bud is cut from a shoot of the previous season's growth by a stroke of the knife tangential to the parent stem so that a little bark and wood, including the cambium at the base of the bud, are removed with it. A T-shaped cut is then made through the bark of the stock and the bud is inserted in this wound so that its cut surface is in contact with the wood and the base is under the bark, which is then tied firmly down to secure a good union.

The choice between grafting and budding, between the different methods of performing each, the age of stock and scion, the time of year for the operation, the most suitable stock for a given scion, etc.,

FIG. 145. Method of budding. With a stroke of the knife tangential to the stem a bud with a little bark and wood at its base is cut off from the scion, left. This piece is then inserted under the bark of the stock through a T-shaped opening and firmly tied in place.

are details of horticultural practice varying with the purpose to be attained.

CONSTANCY OF SPECIES IN VEGETATIVE PROPAGATION

Should the plant obtained by vegetative propagation be looked upon as a new plant or as a continuation and extension of the old? This is

but an academic question. It is more important to know whether or not the species and variety after years of such propagation will be like the original. With a few doubtful exceptions there is no permanent change. In grafted trees the stock may affect the scion *temporarily* through a disturbed nutrition, but if scions from this changed tree be grafted onto suitable stocks the original characters will again assert themselves This fact gives vegetative propagation a great advantage over propagation by seeds in the case of some economic plants, such as strawberries and apples, in which new individuals grown from seeds differ from the parent variety. They are the results of cross-pollination at some time in their ancestry and the variety thus formed has not yet become fixed The resulting fruits are likely to be different from the one from which the seed was obtained, and commercially inferior.

Review Questions

1 What is meant by "vegetative propagation'?
2 Is it more nearly universal among the higher plants or the lower plants?
3 Name five kinds of vegetative reproductive bodies or structures
4. Name four ways by which man propagates plants vegetatively
5. Give an example of a plant with specialized stolons
6 How does a stolon differ from a rhizome?
7. How does a rhizome differ from a root?
8. What do rhizomes and tubers have in common?
9. How do bulbs and corms differ in structure?
10. What part of each of the following is stem (1) bud (2) flower, (3) tuber, (4) bulb, (5) rootstock?
11. Name five kinds of specialized stems.
12 What is the difference between homologous structures and analogous structures? Give two examples of each
13 Why are plants obtained by vegetative propagation more likely to resemble their parents closely than plants grown from seed?
14 Explain the fact that some plants can be propagated by layering more easily than by cuttings
16 Name a flowering plant that can be propagated by leaf cuttings
17. Define (1) scion, (2) callus, (3) rootstock, (4) graft hybrid, (5) stock
18. In grafting what is necessary (1) with regard to the fitting of the stock to the scion, (2) with regard to protecting the wound?
19. By means of budding or grafting, how many varieties of fruit can be produced on one tree?
20. Explain why grafting is used in preference to planting seeds for the propagation of fruit trees.

Part Six

THE DIFFERENT KINDS OF PLANTS

CHAPTER XVI

THE PLAN OF CLASSIFICATION

Thus far in this book attention has been focused on the higher plants, with only occasional reference to the lower ones. The student is now prepared to survey the entire plant kingdom, study examples of each group from the lowest to the highest, and see how they are related to each other.

Up to this point scientific names have purposely been avoided, and plants have been referred to only by their common names, examples being used for which common names left no uncertainty as to identity. However, there are many kinds of plants that have no common names, and some common names, such as "blue bell," "tiger lily," and "black oak," are used in different parts of the country for different kinds of plants. This leads to confusion and uncertainty. It, therefore, becomes necessary to introduce scientific names, and these will be used quite generally in the remainder of this book.

The classifying and naming of plants is an enterprise of great magnitude. Nearly 350,000 species have been described and named, more than half of them being seed-bearing plants. In addition to the named species there are doubtless many thousands of seed plants and of lower plants that have not yet been described. Most of these are in the tropics and other out-of-the-way places where botanical exploration is very incomplete, but others close at hand may have been overlooked or mistaken for similar named species. No one person could in a lifetime become familiar with all of them. So we learn to recognize as many as possible of those in which we have the greatest interest, and the others remain more or less strangers to us. As a result we have specialists who concentrate on the naming and classifying of single groups.

When we speak of relationships among plants we refer to their descent from a common ancestry. This may be hard to trace, for the ancestors have long since disappeared, and only exceptionally have they left fossil remains. Therefore, it has been found expedient to use ap-

pearance, or morphology, as an indicator of relationship. This is generally a reliable method.

We have both *natural* and *artificial* systems of classification. A natural system arranges the plants as nearly as possible according to actual relationships—what we speak of as "blood relationships" in animals. For most scientific purposes natural classification is preferred. Artificial grouping makes no pretense of following actual relationship, and the groups may be based on any character that the members have in common. Thus, trees make an artificial group, for the relationship of some of them, for example pine and apple, is very remote. Likewise "insectivorous," or insect-catching plants, thorny plants, and xerophytes are artificial groups made up of unrelated species. Artificial grouping may serve a useful purpose, but it must not be confused with natural relationship.

Tracing Relationships.—Points of similarity and points of difference must both be considered in tracing plant relationship. Plants are alike in some respects but different in others. If they were all exactly alike there would be only one group. If they showed no similarities, no relationships could be found, and we would have to recognize as many kinds as there are individuals. Plant classification, then, is based on both similarity and difference. Usually a combination of characters, rather than a single character, is required to establish relationship. To put together in one family all plants with compound leaves, or even with pinnately or with palmately compound leaves, would give us an artificial grouping rather than the natural grouping which we are seeking, as it would associate such unrelated plants as walnut, mountain ash, peas, and even ferns; but plants that have compound leaves and also pea-like flowers and pods for fruits constitute the Leguminosae, or pea family, which is a natural group.

In the determination of relationships, reproductive parts—flowers and fruits in higher plants, and simpler reproductive bodies in lower plants—are of greater significance than vegetative parts—leaves, stems, etc.; but the details of the fibrovascular system have been found a useful guide in some cases.

The grouping of plants is usually based on a combination of characters rather than a single one, and occasionally too much emphasis on a single morphological character has misled us into assuming relationship that does not exist. One of the best-known systems of classification places together those trees and shrubs the inflorescence of which is an ament or catkin. This character taken alone would indicate a relation-

ship between willows, birches, and a considerable number of other woody plants that is not supported by the kind of pistillate flowers, the fruits, the structure of the wood, etc.

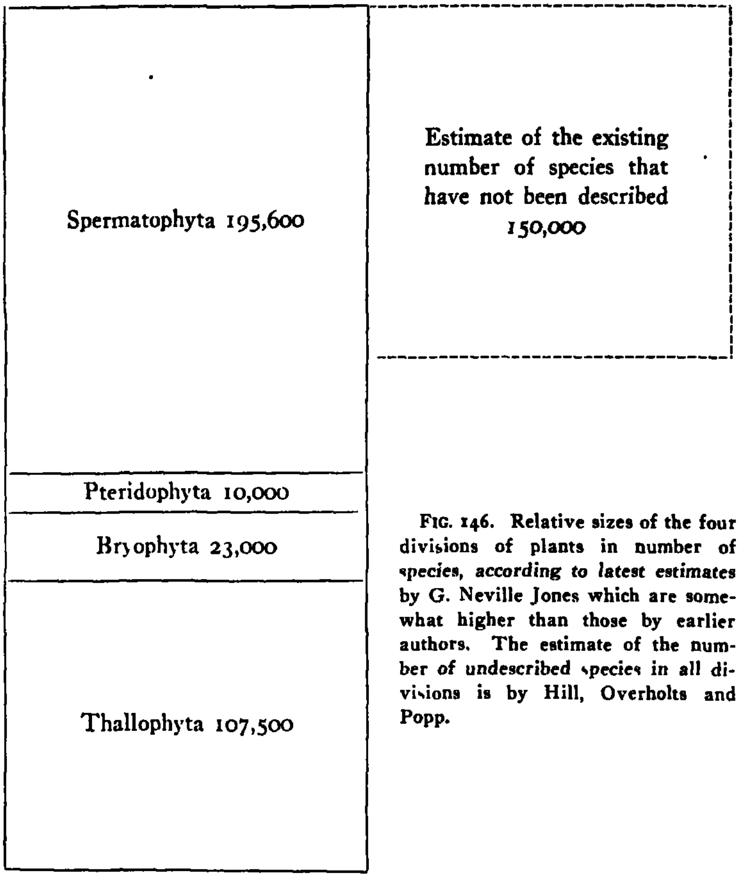


FIG. 146. Relative sizes of the four divisions of plants in number of species, according to latest estimates by G. Neville Jones which are somewhat higher than those by earlier authors. The estimate of the number of undescribed species in all divisions is by Hill, Overholts and Popp.

How the Plan of Classification Works.—The higher plants all have this bond of similarity, that they produce seeds. There are three great groups of lower plants that differ from the higher ones in that they have no seeds. Thus the plant kingdom is made up of four *divisions:* (1) the Spermatophyta or seed plants, (2) the Pteridophyta or ferns and their relatives, (3) the Bryophyta or mosses and their rela-

tives, and (4) the Thallophyta, including all plants below the Bryophyta, e.g., the algae, the fungi, and the bacteria. Each of these four main divisions contains two or more *classes*. There are just two classes of Spermatophyta, the Angiosperms or true flowering plants, such as the apple and tomato, which produce their seeds inside of fruits, and the Gymnosperms, of which the pine is an example, that have no fruits, the seeds being uncovered, and, in the case of our conifers, lying naked on the scales of the cones. Each class is divided into *orders*, each order into *families*, each family into *genera*, and each genus into *species*. The botanical name of a plant is binomial, i.e., it consists of the generic and specific names together. The table of examples on page 213 will serve to illustrate the plan of classification.

FIG. 147. Carolus Linnaeus (1707-1778). Great Swedish naturalist who collected, described and named many plants and animals.

Groups Vary in Size.—In one respect, at least, plants are not standardized. Corresponding groups vary much in size, e.g., not all families have the same number of genera nor all genera the same number of species. The *size of a group* is sometimes measured by the number of members of the next lower group that it contains. For example, a large family is one that has many genera, and a small genus is one that has few species; but more commonly we use the number of species to indicate the size of any group.

It is convenient to have a term to designate all the different group names. They are known as *categories*. Divisions and classes are higher categories, genera and species are lower categories, while orders and families are categories of intermediate rank. *Common* names of species or other groups are not rated as categories.

The plan of classification as set forth above includes only the main categories. In some cases there are others in between these. In very large families it is convenient to recognize two or more *tribes*, each of which is divided into genera. The prefix sub- is often added to the

EXAMPLES ILLUSTRATING THE CLASSIFICATION OF PLANTS

Common Name	*Alfalfa*	Corn	Limber pine	Field mushroom	Black Stem Rust of Wheat
Division	Spermatophyta	Spermatophyta	Spermatophyta	Thallophyta	Thallophyta
Class	Angiospermae	Angiospermae	Gymnospermae	Basidiomycetes	Basidiomycetes
Order	Rosales	Graminales	Coniferales	Agaricales	Uredinales
Family	Leguminosae	Gramineae	Pinaceae	Agaricaceae	Pucciniaceae
Genus	Medicago	Zea	Pinus	Agaricus	Puccinia
Species	sativa	mays	flexilis	campestris	graminis
Botanical name	Medicago sativa	Zea mays	Pinus flexilis	Agaricus campestris	Puccinia graminis

categorical name of a large group. Thus the class Angiosperms (flowering plants) is divided into two *sub-classes,* Monocotyledons and Dicotyledons.

Considerable care and practice will be required to rank the different group names correctly, but this is highly important. Dicotyledon is a sub-class name, not a divisional, class, nor family name. Rosaceae is a family name, not a class name nor a tribal name. It will simplify matters to know that the four divisional names end in *phyta,* the ordinal names in *ales,* and most family names in *aceae.* For class, generic, and specific names there is no such rule. If we wish an indefinite term the word *group* should be used. For example, a division is a group, a family is a group, or certain members of a family may constitute a group. Biennials constitute a group of many kinds of unrelated plants.

In written work generic names should begin with capital letters, but most specific names should not be capitalized, exceptions being those derived from proper names.

Both Naming and Grouping Required.—To some people it might seem sufficient to give plants names without going to the trouble of grouping them. In all scientific work, however, the materials dealt with—chemicals, minerals, heavenly bodies, etc.—are grouped. We can thus learn by inference. For example, when we learn about one kind of acid we can infer that other acids have similar properties; when we learn about one planet the knowledge applies in some measure to other planets; when we become familiar with one kind of a pine tree we apply some of this knowledge to all pines.

Botanical Names versus Common Names.—Those who are not trained in botany are inclined to shrink from the learning of botanical names on the ground that they are too long and hard, preferring to use common names instead. In reality it is the unfamiliar sound of the botanical name rather than its length that makes it difficult. Common names in a foreign language are about as difficult to learn as botanical names. For example, the common name of potato is *Kartoffel* in German, and *pomme de terre* in French, and its botanical name, *Solanum tuberosum,* is scarcely more difficult for English-speaking people.

It should be observed that there is considerable similarity between the common name and the botanical name, one difference being that in Latin the adjective, which is the specific name, comes after the noun, which is the generic name. Thus *Pinus flexilis* will be readily recognized as limber pine and *Nicotiana Tabacum* as tobacco.

It is well recognized that the common name may or may not be

sufficiently exact for scientific purposes. Sugar-beet and peony are not likely to be confused with any other plants, but buttercup, white pine, and bunch grass mean different plants to different people; while the same species of plant, *Aconitum Columbianum*, is variously called aconite, monkshood, and wolfbane.

Most names, both common and scientific, tend to be descriptive, i.e., the name suggests something about the plant. In common names from our own language we easily recognize this, as in yellow bell, white oak, and pop-corn; but if we are unfamiliar with Latin, which is the basis of most scientific names, the specific names such as "vulgaris" (common), campestris (of the field), tomentosa (woolly), etc., may not strike a familiar chord.

Botanical names become easier with familiarity, and the difference between success and failure in mastering them often lies in courage to make the attempt.

Review Questions

1. Give five examples of lower plants.
2. If all plants were exactly alike, how many species would there be?
3. If plants showed only differences from each other and no similarities, how many groups of plants would there be?
4. Do we classify plants mostly by morphological or by physiological characters?
5. Does plant relationship imply origin by direct creation or by evolution?
6. What is the distinction between a "natural" and an "artificial" system of plant classification?
7. What is meant by "categories" or "categorical names"?
8. Arrange the following categories into correct sequence from the largest to the smallest groups: (1) classes, (2) families, (3) species, (4) divisions, (5) sub-classes, (6) genera, (7) orders, (8) tribes, (9) varieties.
9. What general term is used for any collection of similar plants?
10. Give the usual form of ending for: (1) orders, (2) families.
11. Give the common name of any plant and its complete classification in all categories.
12. Which two categories constitute the botanical or scientific name?
13. Which of these should as a rule begin with a capital letter?
14. Why are tribes used in subdividing some families of flowering plants but not others?
15. How many different kinds of plants could properly have the same specific name?
16. If more than one kind of plant had the same specific name, how could they be distinguished one from the other?

CHAPTER XVII

THALLOPHYTA—SCHIZOMYCETES (BACTERIA)

The smallest, the most primitive, and in some respects the most interesting and baffling of all known forms of life are the bacteria. Long after representatives of all other classes of plants had received considerable study, bacteria were still unknown, owing to their small size and the late invention of the microscope.

Discovery.—Bacteria were first seen about 1683 by a Dutch lens maker, Leeuwenhoek, wholly by accident as he was testing his lenses. He was using simple lenses, for, although the compound microscope had been invented a century earlier, it was still crude, and he considered it inferior to his simple lenses for a study of very minute objects. Leeuwenhoek had no conception of the significance of bacteria, and his chief interest in them lay in the fact that although they were so minute yet his lenses were good enough to reveal them. Because some of them swam about, he regarded them as low forms of animal life and so did others for nearly two centuries. Revival of interest in bacteria came in the nineteenth century when it was demonstrated that they were the cause of certain human and animal diseases and that they had an important rôle in decay and in the maintenance of soil fertility.

Morphology of Bacteria

In modern studies of bacteria the organisms are generally kept in *pure cultures,* i.e., one species only is grown on suitable food in convenient containers, such as test tubes closed with cotton stoppers which admit air but keep out dust, other bacteria, and mold spores.

Bacillus subtilis.—One of the larger kinds of bacteria is *Bacillus subtilis,* a harmless species commonly found in decaying vegetation, sewage, and fertile soil. If examined in the living condition with a microscope of very high magnification, this organism affords an interesting study.

Each individual is a single cell, which is cylindrical or rod-shaped with rounded ends. Sometimes two or more may be attached end to

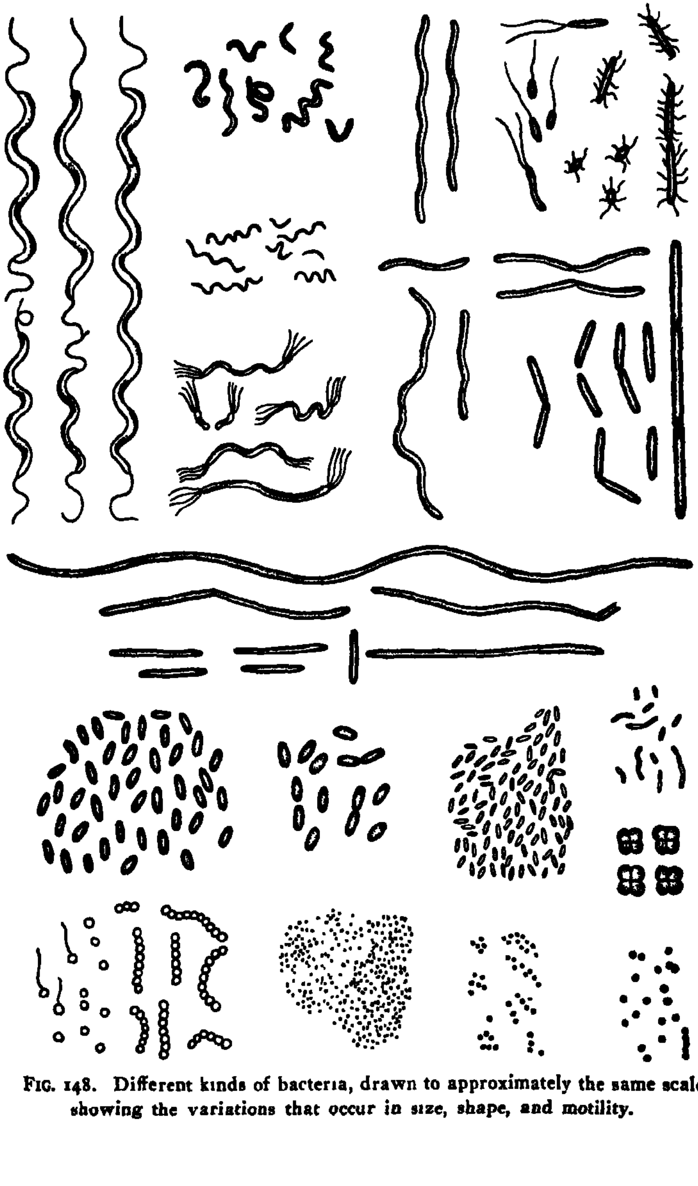


FIG. 148. Different kinds of bacteria, drawn to approximately the same scale, showing the variations that occur in size, shape, and motility.

end in a chain. The more active individuals swim through the liquid in which they are mounted with a slow, waddling movement. Collisions are frequent but not serious. Among the rods will be found some without locomotion, that have their protoplasm drawn to the center and covered by a thick, refractive, inner wall. These are bacterial spores. In the living condition no cell organs can be seen, not even the organs of locomotion.

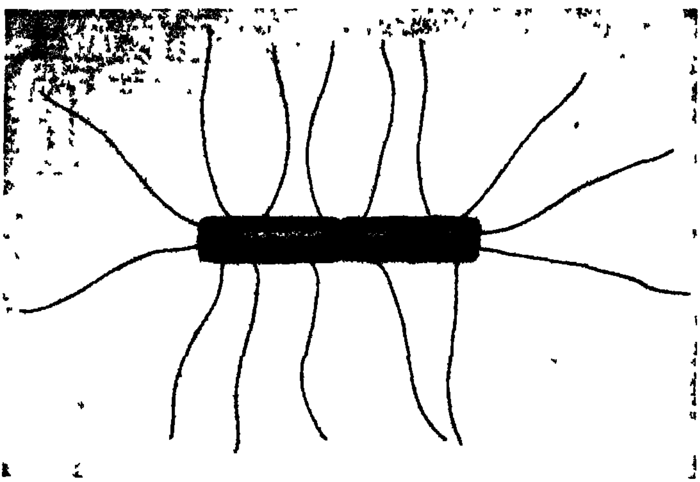


FIG. 149. *Bacillus subtilis,* showing shape of cells and position of flagella

Spirillum rubrum.—This species, likewise a harmless inhabitant of decaying organic matter, presents a more lively picture. The cells are in the form of long, slender, spiral rods that dart about with astonishing agility, rolling over and over sidewise as they move through the liquid. They produce no spores. This species is not nearly so common in nature as *Bacillus subtilis.*

Streptococcus lactis.—This organism, found in sour milk, and the chief cause of the souring, is less exciting to watch. The cells are spherical or slightly elongated in shape, often attached to each other in short chains, and without locomotion. They likewise produce no spores.

The three species just described illustrate most of the morphological features found in the bacterial world. In form there are straight rods, spiral rods, and spheres. Some have locomotion and some have not. Some produce spores, but most do not. Most species are colorless but

Spirillum rubrum is light red when seen in dense masses. All of these species are harmless, but hundreds of others cause disease in plants, animals, or man.

Size.—The size of microorganisms is usually expressed in *microns*, a micron being one-thousandth of a millimeter. Bacteria are spoken of as the smallest of living things, but different species vary widely in size. A few are 30 to 40 microns or more in length, while others are only a fraction of one micron. *Bacillus subtilis*, somewhat larger than the average, measures about one by four microns.

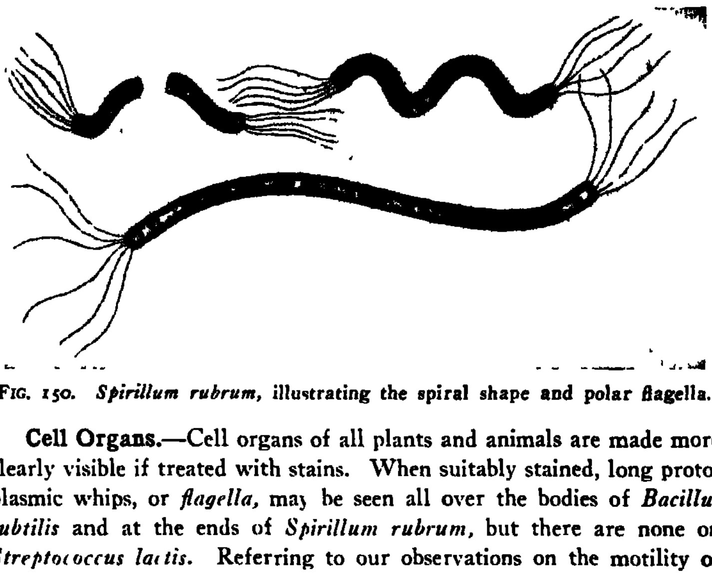


FIG. 150. *Spirillum rubrum*, illustrating the spiral shape and polar flagella.

Cell Organs.—Cell organs of all plants and animals are made more clearly visible if treated with stains. When suitably stained, long protoplasmic whips, or *flagella*, may be seen all over the bodies of *Bacillus subtilis* and at the ends of *Spirillum rubrum*, but there are none on *Streptococcus lactis*. Referring to our observations on the motility of these three species, we infer that these flagella are organs of locomotion.

Bacteria have cell walls which are not made of cellulose, for they have some nitrogen in their composition, an element which cellulose does not contain.

Nuclei of the type that occurs regularly in most plants and animals are not commonly found in bacteria. A few investigators have reported bodies in certain bacterial species that they regarded as such nuclei, but much more commonly there may be seen a few scattered granules that appear to be made of chromatin material. In most bacterial cells no such granules are visible, but it is probable that chromatin in some

form is present in all of them, as they all show strong hereditary tendencies. As the chromatin is not enclosed by a nuclear membrane but is distributed through the cytoplasm, the term *diffused nucleus* has been applied to the chromatin that each cell contains.

Physiology of Bacteria

What bacteria can do and how they live are quite as interesting as what they look like and of much greater practical importance.

FIG. 151. *Streptococcus lactis.* Nearly round, non-motile organisms commonly responsible for the souring of milk.

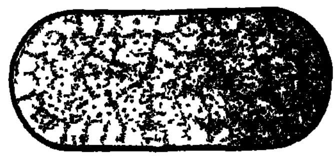


FIG. 152. One conception of the structure of a bacterial cell. The chromatin material, shown by fine dots, is diffused throughout the cytoplasm. (From Swingle's *General Bacteriology*. D. Van Nostrand Co., Inc.)

Reproduction.—The only known method of reproduction in bacteria is asexual. The cells divide by constriction, which in this case is the same as *fission* since the cell is thus divided equally. In some species the cells divide with such frequency that the rate of increase is astonishing. Some species form spores, but as each vegetative cell forms but one spore and each spore changes again into one vegetative cell this process is not regarded as reproduction. These bacterial spores are highly resistant to injurious conditions—heat, freezing, drying, light, chemicals, etc.—and serve to protect the organism against them.

Nutrition.—Except for a few species bacteria are dependent on other plants or animals for food. Lacking chlorophyll they are unable to manufacture carbohydrates but are dependent on supplies already made. Organisms that live on other species and obtain their food from the living cells of their hosts are *parasites*. Those that obtain their food from non-living organic materials of plant or animal origin are *saprophytes*. Enough has already been said to indicate that the three species mentioned at the beginning of this chapter are saprophytes. Many

species can live either parasitically or saprophytically as opportunity affords.

Bacteria have considerable power of digesting solid organic matter. If such materials are decaying, it is because these and other simple organisms are digesting them. In this digestive process the solid foods are not taken into the cells of the bacteria, but rather the digestive fluids secreted by the bacteria are discharged into the surrounding material and there the digestion takes place.

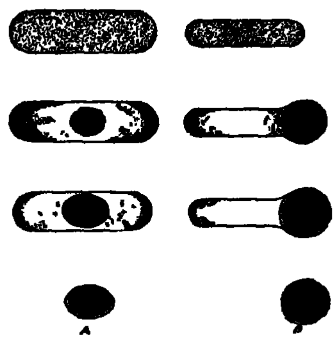


FIG. 153. Stages in spore formation in bacteria. A, *Bacillus subtilis;* B, *Clostridium tetani.* (From Swingle's *General Bacteriology,* D. Van Nostrand Co., Inc.)

Moisture is highly essential for the welfare of all bacteria. Without an abundant supply of it they cannot take up food, reproduce, or carry on their other activities.

Chemical Products.—Economic interest in these organisms is largely dependent on their chemical products. They produce digestive fluids, acids, gases, poisonous toxins, and a considerable number of other chemicals. The ability of *Bacillus subtilis* and *Spirillum rubrum* to decay vegetation, of *Streptococcus lactis* to sour milk, and of *Streptococcus pyogenes* to cause scarlet fever is dependent on the power of these bacteria to bring about chemical changes.

Vitality.—In general, bacteria are sensitive to dryness, light, heat, freezing, and chemical disinfectants. Some are easily and quickly killed by these destructive agents, but those species that produce spores are much more resistant than the others. Some bacterial spores can withstand boiling water for several minutes and freezing and drying for years. Fortunately most disease-producing species do not form spores.

Classification

In modern times most people, in this country at least, have some notions about bacteria. A guess as to how many different kinds there are would bring a wide range of answers. According to the best authorities there are more than thirteen hundred known species, and probably hundreds more will ultimately be described.

We may have some idea of what characters are used in classifying the higher plants—leaves, stems, flowers, fruits, seeds, etc.—but how about the bacteria that have no such structures? Morphology is used to some extent—size, shape, motility, spore formation, etc.—but it has been found expedient to supplement these with physiological characters—what the bacteria can do, their food requirements, their chemical products, the diseases they cause, etc.

Briefly summarizing, the whole group of bacteria belongs to the division Thallophyta and constitutes the class Schizomycetes. This class is divided into seven orders, which in turn are made up of families, genera, and species, in accord with the classification plan presented in the preceding chapter.

Occurrence

The general conception is that bacteria are found everywhere, especially in dirt and filth. This, however, is but another way of saying that bacteria live on organic matter, digest it for their own food, and multiply in it. Probably the upper foot of soil contains more than half the bacteria of the world. Ten million individuals per gram is not an unusual number. Naturally some are found on all exposed surfaces, in practically all water, and in the digestive tracts of all animals.

Economic Significance

Just as some condemn the human race because none of us are perfect and some of us are rogues, so there is a tendency to look upon bacteria in general as enemies of mankind, but no bacteriologist ever entertained such a philosophy. A. Magnin, a French writer on bacteria, said of them in 1878, "It is thanks to them that the continuation of life is possible on the globe." Pasteur realized the usefulness of some of these microorganisms even before he discovered that others cause disease.

Agents in Soil Fertility.—The fertility of the soil is dependent on a number of factors, in three of which bacteria play a major rôle: (1) Organic matter must be decayed and incorporated into the soil.

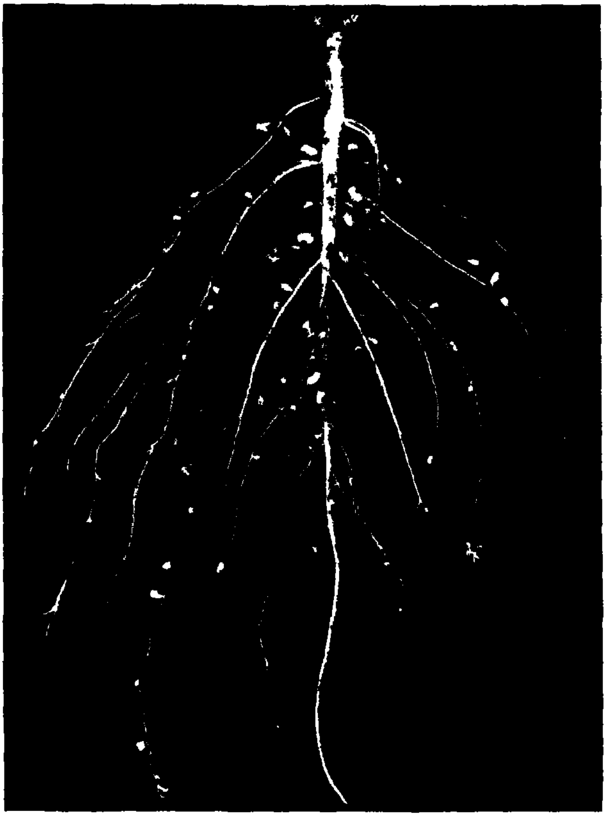


FIG. 154. Nodules on the roots of Alsike clover inhabited by nitrogen-fixing bacteria.

(2) Nitrates must be formed from the nitrogenous portion of this organic matter. (3) The free nitrogen of the air must be recovered and made available for higher plants. Should bacteria disappear from the earth or fail to function, at least three things would happen in a relatively short time: (1) Bodies of plants and animals would accumulate, being only slowly and imperfectly decayed by molds, etc. (2) At

intervals these masses of refuse would be destroyed by great fires. (3) The soil would become barren and cease to produce higher plants, without which man could not live.

How bacteria function in maintaining the soil fertility can briefly be stated.

1. Decay and ammonification. By their digestive secretions such organisms as *Bacillus subtilis*, aided by cellulose-destroying bacteria and

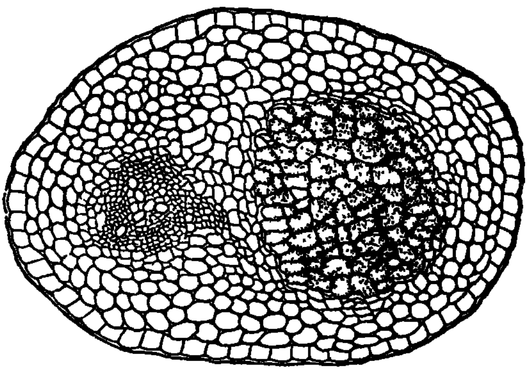


FIG. 155. Internal structure of a nodule showing bacteria in the cells of the roots. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Knudson.)

molds, decompose the dead leaves, etc., and change the protoplasm and stored proteins into ammonia, a process termed *ammonification*.

2. Nitrification. Other bacteria, of which there are few species but innumerable individuals, change the ammonia into nitrates, the form of nitrogen that is consumed in greatest quantity by higher plants. This process of *nitrification* prevents the accumulation of ammonium compounds in the soil.

3. Nitrogen fixation. One genus of bacteria, *Azotobacter*, living in the soil is able to take free nitrogen from the air and use it in the manufacture of nitrogenous compounds. This process is termed *nitrogen fixation*.

Another genus, *Rhizobium*, fixes nitrogen in cooperation with flowering plants of the family Leguminosae, which includes peas, beans, clover, and alfalfa. These organisms, living in the soil, attack the root-hairs and roots of their host and behave in some respects like parasites. They live within the host cells, killing some of them and stimulating others to

abnormal cell division, with the formation of root *nodules*. The bacteria living within these nodules take nitrogen from the air in the soil and combine it with other elements to form compounds, some of which are used by the bacteria and others by the host plant, which grows much more vigorously than it could have done without the bacteria. Thus the legume furnishes good living conditions and a supply of chemical energy for the bacteria which, in turn, help to feed the legume. Such a relationship of mutual helpfulness between two species is termed *symbiosis*. *Rhizobium*, in conjunction with leguminous plants, is said to carry on symbiotic fixation of nitrogen in contrast with the non-symbiotic fixation carried on by *Azotobacter*.

So important is this process of supplying nitrogenous compounds to the soil that inoculation of seed or soil is extensively practiced in those regions where the soil is not naturally supplied with these bacteria.

Bacteria in the Dairy Industry.—Few materials make a more suitable food for bacteria than milk. It is not strange, then, that the influence of bacteria should be felt in the production of milk, butter, and cheese. *Streptococcus lactis* is most in evidence, for it rapidly changes the milk sugar into lactic acid and thus sours the milk. Other species also are capable of spoiling milk, but their action is less rapid and therefore not so noticeable. Epidemics of typhoid fever, scarlet fever, undulant fever, septic sore throat, and a few other diseases have been traced to milk that had accidentally become contaminated, but they are infrequent, especially since more and more use is made of pasteurization.

In cheese manufacture *Streptococcus lactis* and related organisms play an essential part in imparting the desired flavor and consistency.

Food Spoilage.—Bacteria make use of organic matter for food wherever they find it, if conditions are favorable for their action. Naturally they do not discriminate between organic refuse and materials that human beings intend for food. Canning, refrigeration, and drying processes are designed to prevent the inroads of bacteria and molds.

Disease Production.—Of the thirteen hundred described species of bacteria, about one hundred cause diseases of plants, and perhaps as many others cause diseases of man and other animals. The majority of these diseases are rather unimportant, or of rare occurrence, but a considerable number are real scourges of the human race, or are highly destructive to domestic animals or cultivated plants. Naming a few of the more important of these we have: leprosy, tuberculosis, pneumonia, Asiatic cholera, and typhoid fever in man; tuberculosis, anthrax, con-

tagious abortion, glanders, and black-leg in domestic animals; and fire blight, bacterial soft rot of vegetables, crown gall, bacterial blights of beans, and black rot of cabbage in cultivated plants. Not all infectious diseases, however, are caused by bacteria, other minute forms of life being responsible for some.

From this discussion it may be seen that man's relationship with the bacteria is a tremendously vital one. It has developed the subject of bacteriology, really a branch of botany, as a separate science.

Review Questions

1. Do bacteria belong to the animal kingdom or to the plant kingdom?
2. Name the lowest *division* of the plant kingdom.
3. Where are bacteria most abundantly found?
4. Give a brief account of the discovery of bacteria.
5. Name the three shapes commonly foun among bacterial cells.
6. Give the generic and specific names of a bacterial organism illustrating each shape.
7. Give the name of a motile bacterium and of one that is non-motile.
8. Explain how motile bacteria move.
9. What is known concerning the nuclear structure of bacteria?
10. Describe the reproduction of bacteria.
11. How do most bacteria obtain their organic food?
12. What is the explanation of decay in organic materials?
13. State the distinction between saprophytes and parasites.
14. Give an approximate idea of the relative number of bacterial species that are saprophytic and parasitic.
15. Give the generic and specific names of five kinds of bacteria and indicate which of these are parasitic.
16. State three ways in which some bacteria are beneficial, and two ways in which some are harmful to man.
17. Define: (1) flagella, (2) cilia, (3) diffused nucleus, (4) saprophyte, (5) parasite, (6) symbiosis.
18. Name five chemical changes brought about by bacteria.
19. It is known that bacterial multiplication has been going on in the soil for millions of years, and yet the number remains fairly constant. Explain.
20. In what respects are decay and digestion alike?

CHAPTER XVIII

THALLOPHYTA—MYXOMYCETES (SLIME MOLDS)

When collecting in damp woods in the summertime, one occasionally finds on fallen trees or old stumps delicate whitish masses of slimy, naked protoplasm. These are slime molds, or myxomycetes, in the active condition. If seen again the next day the shape and position of the mass will have changed somewhat. At this stage it avoids the light and retreats under leaves, beneath the bark of logs, or into tiny crevices of rotten wood. Partly because of their small size, and partly because they are hidden from view, slime molds are generally overlooked by the inexperienced collector. Later in the season they will be found drawn up into compact reproductive bodies. These reproductive bodies are *sporangia,* or spore-cases, that contain myriads of minute, one-celled spores. There are hundreds of species of Myxomycetes and they show considerable variation in their sporangia. The prevailing color is brown, but some are yellow, red, or purple. They tend to be spherical but other shapes are found. Many, but not all, are mounted on stalks. In size few are as large as peas and many are much smaller, but one species produces a spore mass two inches or more in diameter. If they are broken open there is released a tiny cloud of dry, powdery spores which become widely scattered by the wind. Most of them fall in unfavorable places and die, but a few may be more fortunate and produce new slime molds.

Vegetative Condition.—The term slime mold is quite descriptive of the class Myxomycetes. The plant body during its period of growth is called a *plasmodium.* It is a flat, thin mass of protoplasm without cell wall, creeping slowly over the substratum. The margin is very irregular, and, as a rule, there are many openings, which often give a lace-like appearance to the mass. The plasmodium is a relatively large, naked protoplast several inches in diameter, without chlorophyll, and usually gray or yellow in color. The cytoplasm contains thousands of nuclei as well as numerous vacuoles. The plant creeps along very slowly, absorbing food from the organic matter with which it comes in

contact and surrounding bits of solid food, which become enclosed in vacuoles where the digestible portions are absorbed.

As the plasmodium moves along, parts may become separated from each other, or, on the other hand, two or more plasmodia may come into contact and unite. Cases have been reported, however, in which two

FIG. 156. Fruiting bodies of different kinds of Myxomycetes. (From Kerner's *Natural History of Plants*, Blackie & Son.)

plasmodia of *different species* have encountered each other and remained distinct, refusing to unite. Most of the growth of the plant takes place when in this vegetative condition, and the nuclei increase in number by mitosis. There may be thousands or even hundreds of thousands of nuclei in one plasmodium, which is, in reality, a large cell without a wall.

Reproduction.—Later in the season, when the plasmodium has attained full size and maturity, it moves to a higher, drier, better-lighted place and contracts to form one or more definite fruiting bodies. By cleavage furrows extending in from the surface and sometimes from the vacuoles, the protoplasm is divided into tiny reproductive spores which

secrete protective *cellulose* walls about themselves. Between the spores is a network of non-living material, the *capillitium*, which is made up chiefly of foreign materials that have accumulated in the vacuoles. The spores remain dormant for a time, generally throughout the winter, and sometimes for more than one year. When conditions become favorable

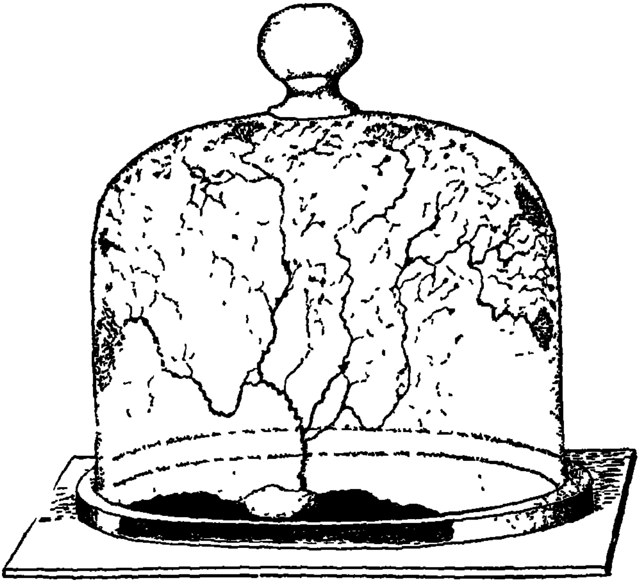


FIG. 157. Plasmodium of a Myxomycete creeping along the inner surface of a bell jar. (From Mottier's *Textbook of Botany*, P. Blakiston's Son & Co.)

they germinate. In this process of germination the spores swell and burst their walls and a tiny protoplast creeps from each one. These naked cells are called *myxamoebae*, because of their resemblance to the amoebae of the animal kingdom. They are somewhat irregular and changeable in shape. At this stage different species show considerable variation in behavior. In some a flagellum is developed, and an actively motile *zoospore* results. This may divide to form others, or it may change back into another myxamoeba or into a gamete.

In some species that have received careful study it has been found that the myxamoebae or the zoospores show a tendency to become gametes, and that these unite in pairs and form zygotes. The cytoplasm

from the two mingles and the nuclei unite into one, although the chromosomes remain distinct for a time, thus giving rise to the diploid number which persists throughout the plasmodial condition. A little later the zygotes that happen to be close together unite to form a plasmodium, but this is not a process of conjugation since the nuclei of the uniting zygotes do not fuse.

Reticularia Lycoperdon.—This species of slime mold has been the subject of careful research. It is one of the simplest of the class. The fruiting bodies are an inch or so in diameter and biscuit shaped, with a slightly roughened surface that looks as if it were coated with gray ashes.

When the spores germinate, the protoplasts that come from them are somewhat irregular and show amoeboid movement for a short time. They probably correspond to the myxamoebae of other slime molds, even though they soon change into a different condition. In a few minutes they take on a definite, elongated, pear shape and send out a single flagellum from the smaller, anterior end. These zoospores are actively motile. They increase in number by transverse constriction, a process which is repeated three or four times.

Without change of form some of the zoospores later show a tendency to unite in pairs, thus indicating that they have become gametes. Each resulting zygote then forms a tiny plasmodium which unites with others, if there are any near by, to make a larger one. Following the conjugation process and during the plasmodial stage zoospores may be gathered up and consumed as food. After growing for a few days the plasmodium, now much enlarged, draws up into one or more sporangia which form spores by cleavage.

The nuclei of the plasmodium each have eight chromosomes, which is the diploid number for this species. Just before the formation of spores the number is reduced to the haploid number of four, which is found in spores, myxamoebae, zoospores, and gametes. By the union of gametes the haploid number is again changed to diploid.

Life History.—It is impossible to fully comprehend a plant without knowing all its stages of development. These stages, taken in their regular sequence, constitute a life history or life cycle. A complete life history consists of a description of the plant at each stage of development, both vegetative and reproductive, and an account of the method of transition from one stage to another. A simple Myxomycete, like *Reticularia Lycoperdon,* has the following life history. The vegetative condition is a flat, gray, naked plasmodium several inches in diameter.

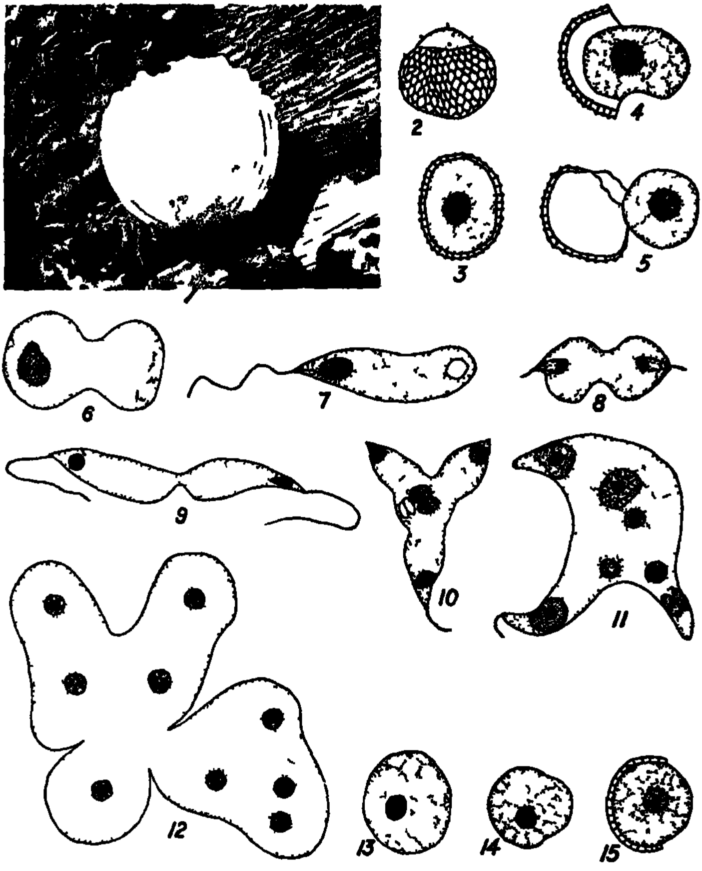


FIG 158 *Reticularia Lycoperdon* 1, mature fruiting body on a log, 2, spore, external view, 3 spore internal view, 4, spore germinating, 5, protoplast which has escaped from spore wall, 6 simple myxamoeba, 7, zoospore, 8, dividing zoospore, 9 fusion of two gametes, 10, 11, three zygotes uniting to form a plasmodium, 12 highly magnified portion of protoplasm inside fruiting body, dividing by cleavage to form spores, 13 young spore before wall is formed, 14 spore with young wall, 15 nearly mature spore (From Malcolm Wilson, *Transactions of the Royal Society of Edinburgh*, Volume 55)

Following a period of growth, the plasmodium draws up into a compact mass which divides into spores by cleavage. When favorable conditions arise these spores germinate to form naked myxamoebae. The myxamoebae soon change into zoospores which divide to form others, and finally some or all of them become gametes. The gametes conju-

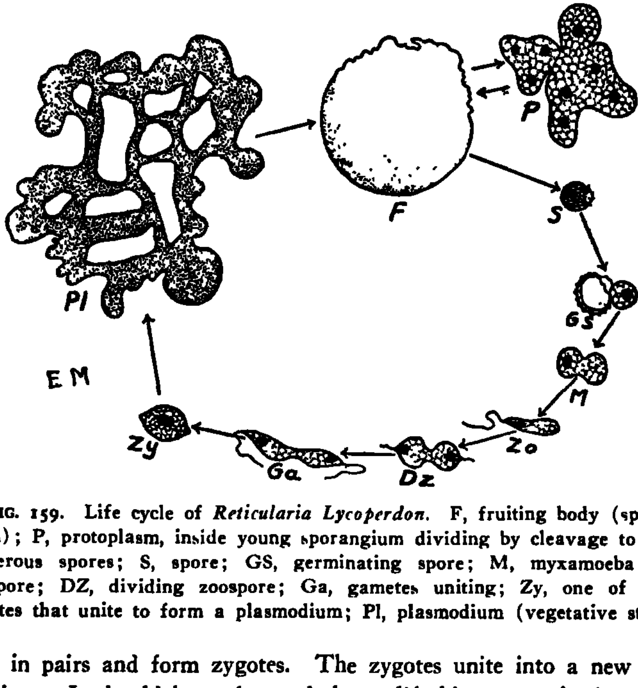


FIG. 159. Life cycle of *Reticularia Lycoperdon*. F, fruiting body (sporangium); P, protoplasm, inside young sporangium dividing by cleavage to form numerous spores; S, spore; GS, germinating spore; M, myxamoeba; Zo, zoospore; DZ, dividing zoospore; Ga, gametes uniting; Zy, one of many zygotes that unite to form a plasmodium; Pl, plasmodium (vegetative stage).

gate in pairs and form zygotes. The zygotes unite into a new plasmodium. It should be understood that a life history can begin at any stage of development, but it must run through to the same stage again. It is customary to begin with a description of the vegetative structure and follow this with a brief account of the different methods of reproduction.

A very briefly worded life history would be as follows: (1) plasmodium, (2) sporangia, (3) spores, (4) myxamoebae, (5) zoospores, (6) gametes, (7) zygotes, and (1) plasmodium again. Such a cycle merely names the stages. A corresponding diagrammatic life cycle is very convenient. Sometimes miniature pictures are used in connection

with diagrammatic life cycles. This method has desirable features and will be used in subsequent chapters of this book.

Relationships of the Myxomycetes.—There is some evidence that the Myxomycetes came from ancestors like the Flagellata, a class of one-celled organisms that show both animal and plant characters. Their well-developed nuclei place them above the bacteria. Their plasmodial vegetative condition suggests no relationship with the true fungi described in Chapter XX. The method of reproduction and the cellulose walls tend to bar them from the animal kingdom. Until further evidence is available they must be regarded as an isolated class of the division Thallophyta, very close to the animal kingdom.

Economic Significance.—These low plants are probably all saprophytic, but as they are relatively few in numbers they contribute very little to the destruction of refuse by decay. There are several plant diseases, notably club root of cabbage and powdery scab of potatoes, caused by parasites that were formerly classed with the Myxomycetes, but recent evidence indicates that this classification was incorrect.

Review Questions

1. In what environment are Myxomycetes mostly found?
2. What name is used for the vegetative condition of a Myxomycete? Describe it.
3. How does it move about?
4. Give two reasons why one might pass close to Myxomycetes without seeing them.
5. Describe the nuclear structure of Myxomycetes.
6. What kind of nuclear division is found in the plasmodium?
7. By what process of cell division are the spores formed?
8. Give the generic and the specific name of an example of the Myxomycetes.
9. Describe the asexual reproduction in *Reticularia Lycoperdon.*
10. Describe the sexual reproduction in *Reticularia Lycoperdon.*
11. Describe three ways of giving the life history of a plant.
12. Write out a brief life history of *Reticularia Lycoperdon.*
13. In what part of its life history has it haploid nuclei, and in what part has it diploid nuclei?
14. In what stage of the life history does a Myxomycete seek darkness and moisture, and in what stage does it seek light and dryness?
15. What function is served by the capillitium?
16. Give the evidence that Myxomycetes are plants rather than animals

CHAPTER XIX

THALLOPHYTA—ALGAE

The term algae is used as a common name for a large group consisting of four classes of Thallophytes with certain characters in common. (1) They live in water or very wet places. (2) They are relatively simple in structure, without roots, stems, leaves, flowers, or seeds. (3) They utilize the light of the sun for energy to carry on an independent life. (4) Most of them are brilliantly colored by chlorophyll and often by additional pigments.

To appreciate the algae we must understand their living conditions. For the most part they are entirely submerged in water. Their supply of oxygen and carbon dioxide is from that dissolved in the water; hence they need no stomata and are in no danger from excessive transpiration. Light penetrates the water but is absorbed by it to such a degree that its intensity is very low a few feet below the surface. The water contains an abundance of mineral matter—some waters too much. Algae may attach themselves to the bottom, or to rocks or other objects in the water, for anchorage but not for food. Distribution of reproductive bodies—gametes and spores—is by means of water, not air.

FLAGELLATA (MASTIGOPHORA)

The difficulty in making a clear-cut distinction between the lower plants and the lower animals has long been recognized as a very real one. What are the characters that belong to plants, and what are the characters that belong to animals? What characters do they have in common?

Plant and Animal Characters.—Plants and animals are alike in having a protoplasmic basis. Both are composed of living cells with cytoplasm and nuclei that are much alike. The chief characters peculiar to plants are cell walls made of cellulose and related materials, large central vacuoles in mature cells, and the presence of chlorophyll, which gives them relative independence in their nutrition. The chief characters peculiar to animals are locomotion, ingestion of solid food within

the body, and dependence on organic matter already manufactured by other forms of life. However, many plants lack chlorophyll, and a few animals have no locomotion. We do not know of any character by which we can, without exception, infallibly distinguish plants from animals.

A Borderline Group.—The class Flagellata, now called Mastigophora by many zoologists, is one of peculiar interest. The individuals are made up of single cells, sometimes isolated, sometimes associated in colonies. Some members of the class, if considered by themselves, would unquestionably be called plants, and other members would just as certainly be classed as animals. Yet if we compare the different species of Flagellata with each other we see strong bonds of relationship between them, except for a few unusual species that are placed in the class for convenience or because they have not yet been studied with sufficient thoroughness to determine their relationships.

The most important bond connecting the members of the Flagellata is locomotion by means of one or more *cilia*.[1] The group is a fairly large one, containing hundreds of species which show considerable variety in the details of their structure. Some have quite firm walls and a definite oval shape, while others are naked protoplasts with an irregular and changing shape. Some have chlorophyll, some have none. Some ingest solid particles of food, some do not. The fact that they constitute a borderline group is shown by the division into two sub-classes, one predominantly animal-like, the other predominantly plant-like. Even here the distinction cannot be made sharp, for there are species that partake of both animal and plant characters. One of these will be described to illustrate this class.

Euglena viridis.—The body of this organism is spindle-shaped, sharp-pointed at the rear end and rounded at the front end where there is a single cilium. This cilium leaves the body through a funnel-shaped

[1] The terms *cilia* and *flagella* are both used to designate the slender protoplasmic organs of locomotion found on certain cells of the lower plants and animals. If these organs are short and numerous they may be called *cilia;* if long, and few or single, they may be called *flagella,* and this usage is followed by many zoologists. Some would restrict the term flagella to those with a central core surrounded by a layer of different density, and class as cilia all with a homogeneous structure, regardless of their length or number. Botanical usage of these terms is not very consistent. The organs of locomotion on bacterial cells are usually called flagella, regardless of size and number, and those on other plants are usually called cilia, even though there are only one or two on a cell.

gullet. This gullet was once supposed to receive solid food, but there is doubt if such is the case. Near the base of the cilium is a brick-red pigment spot that is sensitive to light. The cell also contains cytoplasm, a nucleus, and a considerable number of disc-shaped chloroplasts, which

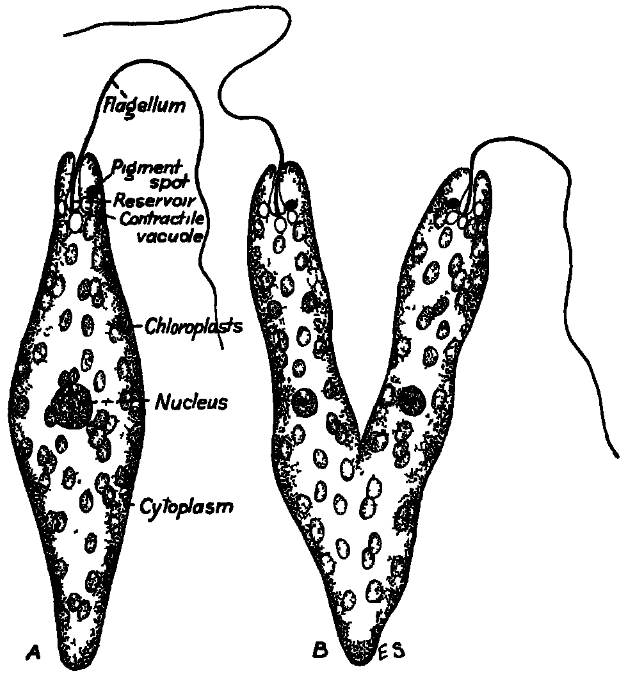


FIG. 160. *Euglena viridis*, representative of the Flagellata. A, mature organism; B, reproducing by longitudinal division

may, however, be absent in certain individuals. There is no cellulose wall and this permits the body to be flexible.

Asexual reproduction is by longitudinal fission, and sexual reproduction is unknown in this and most other species of *Euglena*. Under certain conditions the cell loses its cilium and rounds up into a thick-walled resting spore which later divides to form four active cells.

Significance of the Flagellata.—There is evidence that the Flagellata represent a great ancestral group from which most animals and plants originated. We shall refer to them repeatedly in succeeding chapters. Some of the animal-like flagellates are parasitic on larger animals.

CYANOPHYCEAE (BLUE-GREEN ALGAE)

In greenhouses, on old wet soil that has been left undisturbed, or out of doors where there is a constant splash or drip of water, one often sees little patches of bluish-black growth. Examination of this material with a microscope reveals the tangled threads of a blue-green alga. One of the commonest of these is *Oscillatoria*.[1]

Morphology.—It is very difficult to remove a single plant from the tangled mass, but if one succeeds he has a *simple filament*, i.e., an unbranched thread composed of a single row of cells. Except for a slight tapering at one or both ends, the filament is uniform in character throughout its length. The cells are disc-shaped and arranged like coins

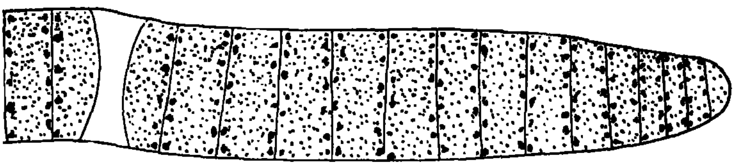


FIG. 161. *Oscillatoria*. Tip of a filament.

in a stack. The color is blue with a slightly greenish tint, and it is diffused through the protoplasm, not confined to plastids. Numerous granules may be seen, most of which are composed of *glycogen*, a carbohydrate similar to starch.

No typical nucleus can be seen, even in properly stained material. There are, however, some chromatin granules suggestive of those found in certain bacterial cells. The term "diffused nucleus" has also been applied to the nuclear granules of the Cyanophyceae, although "central body" is perhaps more used.

Physiology.—*Oscillatoria*, like most algae, requires an abundance of moisture. When actually in the water the ends of filaments protruding from the general mass wave back and forth with a slow, stately motion; hence the generic name.

The blue-green algae live a relatively independent life. With their two pigments, chlorophyll and *phycocyanin*, they manufacture glycogen from carbon dioxide and water, using the light of the sun for energy. They carry on, then, a kind of photosynthesis.

[1] Usually plants are spoken of by their generic and specific names, but it is sometimes convenient to use the generic name alone when the statements made apply to all or most of the species in the genus.

Reproduction in *Oscillatoria* is very simple. There is no sexuality, neither are there asexual spores. The cells divide by constriction and, growing to their original size, elongate the filament; but these processes in themselves produce no new plants. However, accidents occur and occasional cells die and decay. Thus the filaments are broken into pieces of varying length. In some other genera, for example *Nostoc*, cells at fairly regular intervals swell into heterocysts and then die, thus dividing the filament more definitely than is done in *Oscillatoria*.

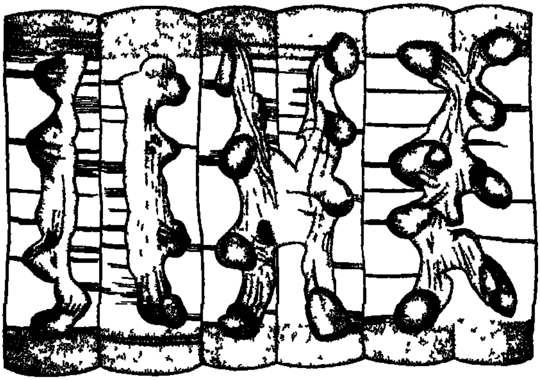


FIG. 162. *Oscillatoria*. Longitudinal section of portion of a filament showing nuclear structure and cell division (Redrawn after Olive.)

Relationships.—The class Cyanophyceae is a small isolated group. Its relationship with other Thallophytes is uncertain. The character of its nuclei and the lack of plastids and reproductive bodies throw doubt upon its close relationship with the other algae. The scattered chromatin bodies in lieu of nuclei and the lack of sexuality suggest a relationship with the bacteria. The bacteria may have evolved into blue-green algae by acquiring pigments, or it may be that some Cyanophyceae evolved into bacteria by loss of pigments. It is even possible that some of the most primitive bacteria, that lived on inorganic matter exclusively, evolved into Cyanophyceae; and that some of these in turn lost their pigments and became saprophytic bacteria, dependent on organic matter.

Economic Significance.—The usefulness of the Cyanophyceae is very limited. They are not sufficiently abundant to contribute much to the organic matter of the soil, although they doubtless add a little. On

the other hand they are sometimes troublesome in water supplies, to which, when they die, they give a disagreeable odor and taste. Fortunately, algae are very sensitive to the presence of copper sulfate, and so this is sometimes added in small quantities to reservoirs in order to suppress them.

Chlorophyceae (Green Algae)

In fresh waters the commonest algae are bright green in color. These are members of the class Chlorophyceae. Their appearance is familiar to all who spend much of their time out of doors, and many people living inland have never seen any other kind. Usually they are looked upon with disdain or even aversion and called "pond scum" and other uncomplimentary names. Under the microscope, however, most of them are beautiful in color and design. A few examples will serve to picture this great class of algae, which in number of species is the largest of the four.

Protococcus

The presence of a light green coating on the sides of old flower pots in the greenhouse, or on the north side of wooden fences and stumps,

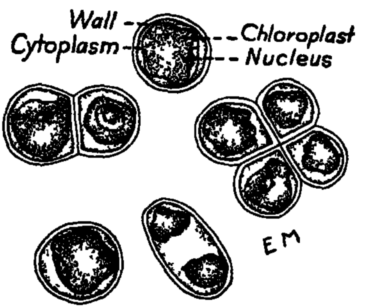


Fig. 163. *Protococcus.* Stages in the formation of temporary colonies by cell division.

is a familiar sight. Lower plants of several kinds may contribute tc these green growths, but the tiny alga, *Protococcus,* is one of the commonest.

The *Protococcus* plant is composed of a single cell. In this cell there is cytoplasm, a well-developed nucleus, and a single chloroplast, which is irregularly hemispherical. The only kind of reproduction known to occur in this alga is cell division by constriction. The cells

resulting from this division may cling together to form groups and colonies. There is no motility.

Chlamydomonas

Far more interesting than *Protococcus* are the tiny, active cells of *Chlamydomonas*. This alga is fairly common in pools of standing water. It has several stages of development that have sometimes been mistaken for different kinds of algae.

Vegetative Structure.—Chlamydomonas is a unicellular alga, the cells of most species being oval in shape. The plant has the power of locomotion by means of two long cilia that protrude through the wall at the smaller end. As this end leads when the cell swims about, it is called the *anterior* (forward) end, while the larger end that follows is called the *posterior* (rear) end.

The cell contains a single cup-shaped chloroplast with the opening toward the anterior end. Embedded in the chloroplast toward the posterior end of the cell is a *pyrenoid,* a light-colored nitrogenous body that aids in starch formation by photosynthesis. The starch is deposited in plates or cakes over the entire surface of the pyrenoid.[1]

In the anterior end of the cell, near the edge of the cup-shaped chloroplast, is a tiny, shining, red body known as a *pigment spot.* It is sensitive to the intensity of the light, but as it cannot actually see objects it should not be called an "eye spot," as was commonly done some years ago. By means of the pigment spot and the cilia the plant is sometimes able to find and move into places where the light is of the most favorable strength for its welfare.

The nucleus is located near the anterior end of the cell and the cytoplasm surrounds both it and the chloroplast. The cell has a very thin cellulose wall.

Reproduction.—Reproduction is preceded by withdrawal of the cilia and consequent loss of locomotion.

In asexual reproduction the nucleus divides by mitosis; the chloroplast also divides, and the cell then divides by constriction, thus forming two *Chlamydomonas* plants enclosed within the wall of the mother cell. In some species this process of division is repeated to form four cells; in others there is a third division, resulting in eight cells which constitute a temporary colony. These newly formed cells are at first

[1] Pyrenoids are found in the cells of most green algae but are not of general occurrence in other algae and are rare in plants above the Thallophyta.

covered only by their plasma membranes, but they soon escape from the old cell wall, enlarge to the original size of the parent cell, and form walls of their own. In exceptional circumstances the escape of the daughter cells is delayed by the presence of gelatinous material, which may increase in volume while the cells continue to divide until a large number have accumulated within the mass of jelly. Eventually they escape as individual plants.

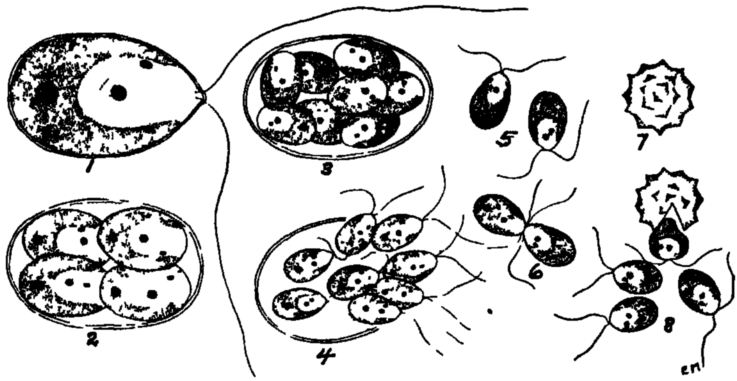


FIG. 164. *Chlamydomonas*. 1, mature cell; 2, four young cells formed in asexual reproduction; 3, eight gametes formed by the division of one cell; 4, gametes escaping from old cell wall; 5, free-swimming gametes; 6, two gametes conjugating; 7, resting zygote; 8, four cells formed from the zygote. Somewhat diagrammatic.

In sexual reproduction the cell of *Chlamydomonas*, after drawing in its cilia, divides as in asexual reproduction, but the process is continued until 16, 32, or 64 very tiny cells are formed. These escape from the old cell wall, push out cilia, and look like the parent cell except for size. Their behavior shows them to be gametes, for they unite with each other in pairs in a process of true conjugation. The anterior ends unite first and for a few minutes they continue to be motile by their four cilia—two from each gamete. Soon, however, the cilia are withdrawn, the protoplasts escape from their cell walls, and a more complete union of the cells takes place, in this way producing a round, nonmotile zygote. This zygote secretes a thick protective wall about itself and for a period of several weeks lies dormant in the bottom of the pool. It then germinates, in this process usually producing four motile daughter cells which escape from the old heavy wall. They soon grow to full size, and the life cycle is complete.

Life History.—*Chlamydomonas* is a unicellular green alga, swimming by means of two cilia. It has two kinds of reproduction. The cells may divide to form two, like the parent but smaller, or each cell may divide into motile gametes which conjugate in pairs. The zygotes thus produced divide later into four tiny plants, each like the original.

Ulothrix

Various species of *Ulothrix* are among the commonest of the green algae.

Vegetative Structure.—The *thallus* or body of *Ulothrix* consists of a simple filament a few inches long and barely visible to the unaided eye. Most of the cells are cylindrical in shape, with one nucleus, one chloroplast, and one or more pyrenoids. The chloroplast is relatively large and shaped like a plate bent around to fit the inner surface of the wall. In cross-section it is somewhat horseshoe shaped.

The basal cell differs considerably from the others in the filament. It contains little or no chlorophyll and is specially shaped for anchoring the filament to the substratum—a rock, a piece of wood, or whatever it may be. This *holdfast* may wrap about a projection of the object or push into a tiny cavity, thus holding the plant from being washed away.

Practically all cells of this alga are capable of elongation and division. Such a process of growth is termed *intercalary*, as contrasted with the *terminal* growth in those plants where only the terminal cell divides.

Nutrition.—*Ulothrix* plants live, for the most part, submerged in water. This water contains mineral matter, carbon dioxide, and oxygen in solution, and these materials are absorbed by all the cells of the filament. The basal cell does not absorb food for the entire plant as do the roots of higher plants. Each cell carries on photosynthesis and lives almost independently of the other cells of the filament.

Reproduction.—The asexual reproduction of *Ulothrix* is well developed. Under favorable conditions motile *zoospores* are formed. These may be produced by any cell of the filament except the basal holdfast, and usually a considerable number of cells form them almost simultaneously. In this process the nucleus and chloroplast divide, and then the cell divides by cleavage until 4, 8, or 16 smaller cells are formed, the number depending on the species. These naked cells within the wall of the mother cell then develop into zoospores by pushing out four cilia each and producing a pigment spot. They escape through a hole in the wall of the mother cell and swim about, looking very much like indi-

viduals of *Chlamydomonas,* except for the number of cilia and the absence of a cell wall. After swimming about for a short time each zoo-

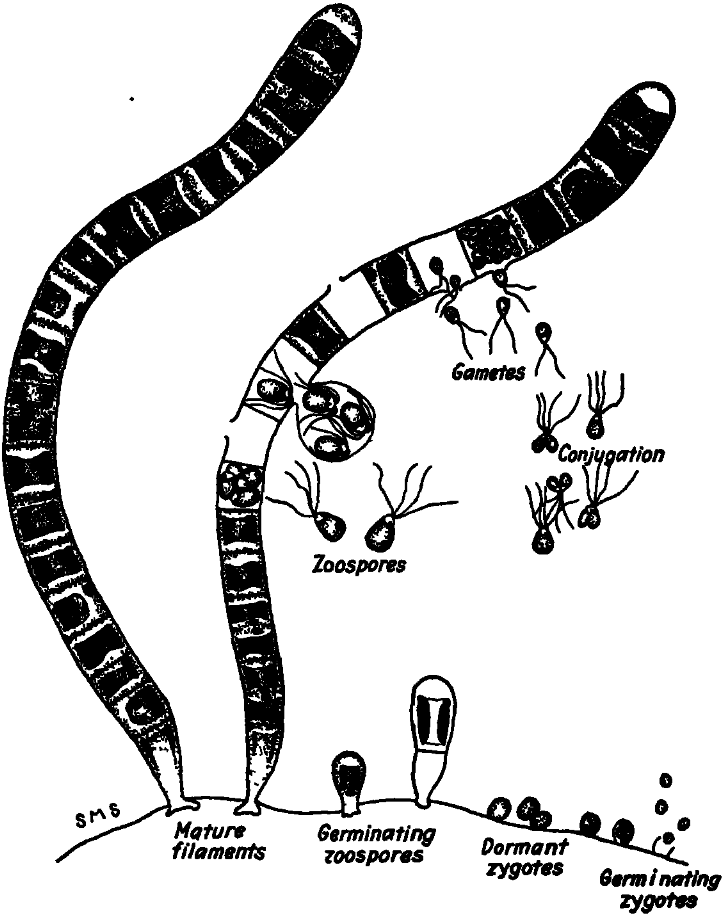


FIG. 165. *Ulothrix.* Stages in development. Somewhat diagrammatic.

spore develops into a new plant, if conditions permit. In this process the cilia are withdrawn, the cell comes to rest on the bottom of the stream or pool, a projection grows downward, forming the holdfast that attaches the plant to the substratum, and a cell wall is secreted about the hitherto naked protoplast. This is the beginning of a new plant. It elongates

and divides by constriction, repeating the process until a full-sized, filamentous plant is formed.

In sexual reproduction various cells throughout the plant divide to form gametes, in most species 8, 16, or 32. These look much like the zoospores except that they are smaller and biciliate. They are released from the cells that produced them, usually during the morning hours, and swim about actively. Here their difference from zoospores becomes evident, for each conjugates with another, if such can be found. For a few minutes after the beginning of fusion the pairs swim about with their four cilia, but as the union becomes more complete the cilia are withdrawn and a thick-walled, resting zygote is formed. After a dormant period the zygote germinates by producing tiny spores, usually four in number. They are non-motile as a rule, and after attaching themselves to some solid object they grow into new plants.

Life History.—In the life history of *Ulothrix* we note that it is a filamentous green alga attached at the base. It has two kinds of reproduction. Asexual reproduction is by zoospores which form in the undifferentiated cells of the filament. After a brief motile period they settle down and develop directly into new plants. In sexual reproduction numerous motile gametes, equal in size, are produced in the cells of the filament. By conjugation with similar-appearing gametes from other cells they form zygotes. After a period of rest each zygote produces four non-motile spores that grow directly into new plants.

Oedogonium

Algae of the genus *Oedogonium* show considerable advancement in morphological specialization over those belonging to *Ulothrix*.

Vegetative Structure.—*Oedogonium* is an unbranched, filamentous, green alga with a basal holdfast cell by which it is normally attached; but masses of filaments frequently become broken away and float on the surface of the water. Each cell of a filament, except for the basal holdfast and the pointed tip, is cylindrical in shape, with a peripheral layer of cytoplasm in which is embedded a chloroplast that wraps around the large central vacuole like a much perforated sheet or a coarse network. It contains several pyrenoids. The single nucleus is sometimes in the peripheral cytoplasm, but often it may be seen suspended within the central vacuole by strands of cytoplasm that extend to the outer layer.

Growth in length is chiefly confined to certain cells and is of an unusual character. Around the protoplast, near one end, a ring of plastic cellulose forms as a thickening of the cell wall. Just below it a cross

wall forms, dividing the cell into two, one much shorter than the other and bounded in part by the newly formed ring. As internal pressure in this cell increases, the lateral wall ruptures all around outside the ring and the cell suddenly elongates, the ring of soft material stretching out and forming a thin side wall around the cell, which soon becomes several times its original length. As a result a sort of cap is formed by the old

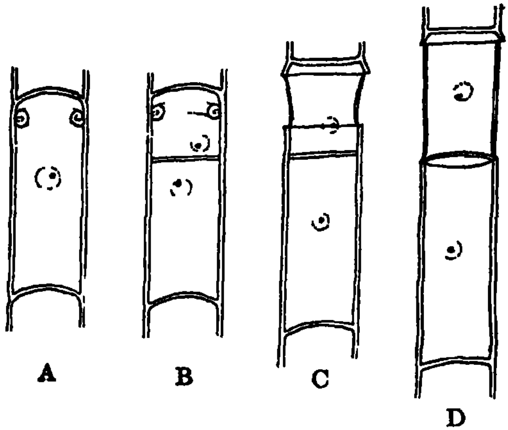


FIG 166 *Oedogonium* Stages in cell division and elongation In A there is a thick, plastic ring of cellulose near one end In B cell division has taken place near the ring In C the old cell wall has broken outside the ring, the cell has elongated, and the ring has stretched out, covering the break. In D further elongation has taken place (From Mottier's *Textbook of Botany*, P Blakiston's Son & Co)

end wall and the remnant of the old lateral wall that was above the line where the break took place This process may be repeated several times, resulting in several successive marks around the growing cell.

Reproduction.—Asexual reproduction is by zoospores that differ from those of *Ulothrix* both in their formation and in their structure. The protoplast of almost any cell of a filament may become a single zoospore, which is consequently relatively large. A considerable number of zoospores are formed by an *Oedogonium* plant and these escape into the surrounding water. A mature zoospore of this plant is oval in shape, with a single nucleus and usually no pigment spot. It is green in color, but has a transparent region at one end. Around the cell, where the green portion joins the transparent portion, is a girdle of cilia, which, by their united action, propel the zoospore through the water,

transparent end foremost. After swimming about for a short time the zoospore comes to rest. The transparent end becomes attached to any convenient object in the water and its cilia are withdrawn. It then

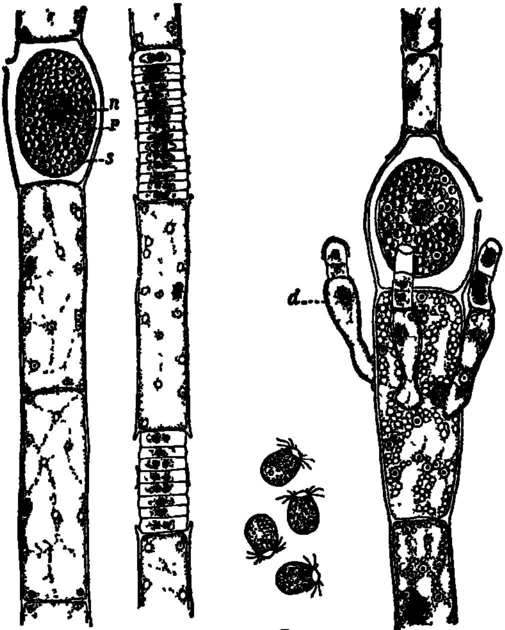


FIG. 167 *Oedogonium.* Reproductive structures A and B, a species in which male and female plants are much alike in general appearance A, portion of oogonial filament containing a zygote: *n*, nucleus; *p*, pyrenoid, *s*, starch. B, portion of an antheridial filament containing two groups of short cells—antheridia. C, a species in which the male plants, *d*, are much smaller than the female plants and are called "dwarf males." Three of these are attached to an oogonial filament. D, zoospores. (From *Elements of Plant Science* by C. J. Chamberlain, McGraw-Hill Book Co., Inc.)

secretes a cellulose wall and divides transversely. The attached daughter cell forms a holdfast for the plant and does not divide again, but the other grows and divides repeatedly, thus forming a new plant.

In sexual reproduction two kinds of gametes are formed. Some species of *Oedogonium* are monoecious, both male and female gametes being produced by the same plant. Other species are dioecious, each

plant producing only one kind—male or female. Much variation in morphological detail is found among the different species.

In some dioecious species, but not all, the plants that form male and female gametes are quite unequal in size, the female plants being much larger. They may also produce zoospores, but the small male plants do not. Here and there throughout the filament *oogonia* are formed. These are containers of female gametes, or eggs. In *Oedogonium* each oogonium contains only one egg, although in some other Thallophytes there are several. The oogonium is formed by the enlargement and rounding up of a newly formed vegetative cell. Its protoplast shrinks away slightly from the oogonial wall and becomes an egg. A pore then forms in the wall of the oogonium through which the male gamete can enter.

The plants that form the male gametes are very small in some species. They come from special small zoospores produced by the female plants. Commonly these zoospores attach themselves to the female filament just below the oogonia and there grow into the *dwarf male* plants. A dwarf male plant consists of a basal cell, bearing at its tip one to three *antheridia,* which contain the male gametes, or *sperm cells*—two or four in each antheridium. A sperm cell resembles a zoospore in appearance but is smaller and has fewer cilia in the girdle.

Responding probably to a chemical stimulus, the sperms when released swim to the pores of the oogonia, where one enters and fertilizes the egg. The zygote thus formed becomes red-brown in color, its starch is replaced by oil, and a heavy wall is secreted about it. It goes into a dormant state which continues for months or even years. When the zygote germinates it produces four zoospores which grow into new plants.

Here we have one of the most highly developed of the green algae.

Spirogyra

One of the most beautiful and most frequently studied of the Chlorophyceae is *Spirogyra.* It is like *Ulothrix* in being a filamentous green alga, but in some respects it is so different that it is placed in a different order.

Vegetative Structure.—The thallus of *Spirogyra* is a simple filament that is free floating, i.e., it does not attach itself to adjacent objects. It cannot be said to have a base and an apex, as both ends are essentially alike. The cells are large and the filaments are long. Often many plants are tangled together in the water and form bright green masses a

foot or more in diameter. By its unattached condition and by the very slippery feeling of the masses of filaments, the collector can distinguish this alga from most others without the aid of a microscope.

The beauty of *Spirogyra* rests largely in its chloroplasts, which are shaped like spiral ribbons with scalloped margins. Each cell contains from one to a half dozen of these spiral bands, the number depending on the species. They wind round and round the cell just inside the plasma membrane. Each chloroplast contains several pyrenoids, which, with their coatings of starch, appear as tiny bright bodies in the chloroplasts. The nucleus is generally near the center of the cell, where it is surrounded by a layer of cytoplasm, strands of which run from this layer out through the vacuolar space and join the peripheral cytoplasm on all sides.

Reproduction.—*Spirogyra* has no true asexual reproduction. The cells divide but remain attached, thus elongating the filament without making new ones. If the filaments are accidentally broken, new individuals are thus formed. The plant has no motile stage in its life history.

Sexual reproduction in most species involves two filaments that chance to lie close together and more or less parallel. The entire protoplast of each cell becomes a single gamete. The wall of each gamete cell bulges outward to form a tube that connects at its tip with a similar one from a gamete cell of the neighboring filament. By the dissolution of the walls of the tubes where they join, a continous passage is formed from one cell to the other. All the gametes from one filament, which are naked and have no cilia, now flow slowly through these tubes to the cells containing the gametes of the other filament, leaving behind the empty cell walls of one filament. Conjugation takes place inside the cell walls of the stationary gametes, the two nuclei unite, and zygotes are thus formed which later develop heavy walls. They are released by the decay of the old cell walls of the filament. After a period of rest the zygote germinates, and a one-celled *Spirogyra* plant creeps forth which, by cell growth and division, develops into a new filament.

In a few species of *Spirogyra* conjugation takes place between adjacent cells of the same filament. In this process the conjugation tubes form by extensions of the lateral walls near the ends of the cells and make a passage around the cross-wall through which one gamete moves to join the other.

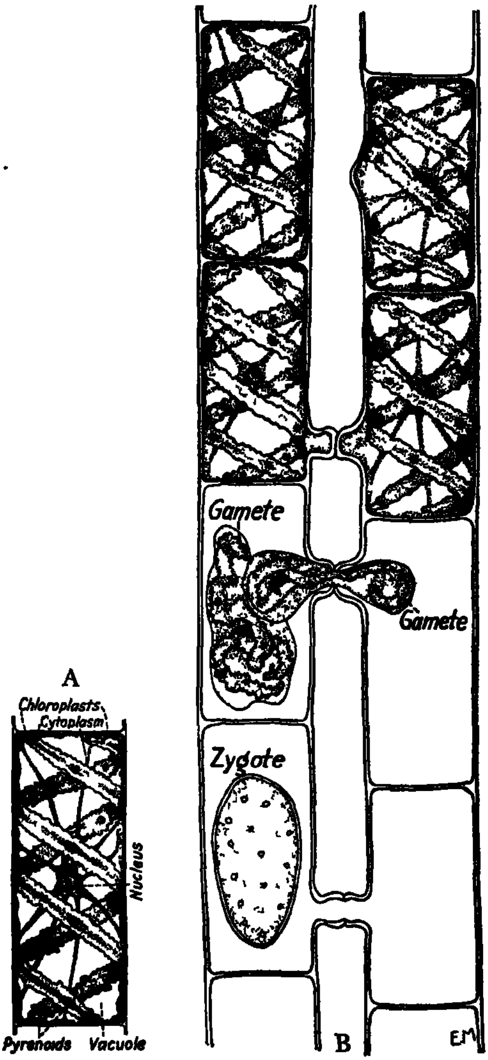


FIG. 168. *Spirogyra*. A, one cell from a filament; B, stages in conjugation. Any protoplast in a filament may become a gamete and conjugate with one in a neighboring filament or, in some species, with an adjacent cell of the same filament.

Vaucheria

Vaucheria is one of the commonest of the green algae. It may be found in standing or running water, but it is rather common in the sod of marshy grass land. It can often be recognized by its felt-like masses,

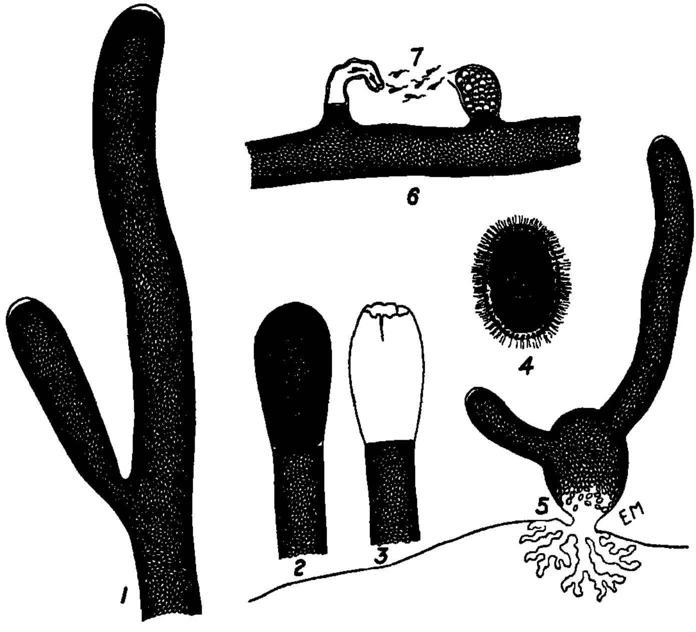


FIG. 169. *Vaucheria.* Stages in development. 1, tip of branching filament; 2, formation of zoospore; 3, tip from which zoospore has escaped; 4, multinucleate and multiciliate zoospore; 5, young plant developing from zoospore that has come to rest; 6, branch bearing antheridium and fertilized oogonium; 7, motile sperms.

which are rough in texture, and by its color, which is a darker green than that of most algae.

Vegetative Structure.—The thallus of *Vaucheria* is a much-branched filament growing from a transparent holdfast. The internal structure of the filament is strikingly different from that of *Ulothrix* and *Spirogyra.* It has practically no cross-walls but many nuclei and many tiny, flattened, oval chloroplasts. It may be interpreted as being a very large multinucleate cell. Plants with such a structure compose

several genera of the Thallophytes and are called *coenocytes*. *Vaucheria* has no pyrenoids and forms oil rather than starch.

Asexual Reproduction.—When conditions are favorable, cross-walls are formed near the ends of the branches. The new cells thus formed develop into zoospores, one in the tip of each branch. Some interesting work has been done on the physiology of zoospore formation. Often weeks or even months elapse with no indication of asexual reproduction. It has been found, however, that if the filaments are partially dried, then soaked in water, or are kept for a short time in nutrient solution and then changed to pure water, or sometimes if they are changed from running water to standing water, zoospores will promptly be formed during the following night and released the next morning. These zoospores escape by the rupture of the walls at the tips of the branches. The zoospores of *Vaucheria* are of relatively large size. They are green in color, oval in shape, multinucleate, without pigment spots, and covered with many cilia which are produced in pairs, each pair associated with a nucleus. After swimming about for a short period, they settle down and withdraw their cilia. A projection then extends downward to form a holdfast, and one or two branches extend upward and grow into a new plant.

Sexual Reproduction.—*Vaucheria* forms more specialized reproductive structures than do the algae previously described. Certain organs bear female gametes and are called *oogonia;* others on the same filament bear male gametes and are called *antheridia.* In *Vaucheria sessilis* the structures are somewhat simpler than in some other species. At various places on the sides of the filaments a single oogonium and an antheridium are produced close together. The oogonium is pear-shaped with a transparent tip. While it is forming it contains many nuclei, but all except one migrate back into the filament or disintegrate. By a wall across the base of the oogonium a single *egg cell,* or female gamete, is partitioned off from the filament. The antheridial branch is more slender and bent. The multinucleate contents of the antheridium divides into numerous tiny *antherozoids,* or male gametes. Each antherozoid is an elongated, oval, colorless cell, with a single nucleus and with two cilia attached to the side. The antherozoids are attracted to an opening in the transparent tip of the oogonium into which one swims and fertilizes the egg cell. After a period of dormancy, the zygote germinates directly into a new plant.

Development of Sexuality in the Chlorophyceae

The Chlorophyceae illustrate the evolution of sexuality better than any other class of plants. If the gametes are of the same size and appearance they are called *isogametes.* Such gametes are found in *Chlamydomonas,* in some species of *Ulothrix,* and in many other algae. The simplest situation among isogametes would be one in which any gamete would conjugate with any other gamete, i.e., there would be no distinction of any kind between male and female. Possibly such gametes occur in some simple algae, but there is growing evidence that in most species, perhaps all, there is at least a *physiological* difference even among isogametes. Certain ones that might be called male or female, as the case may be, will not unite among themselves but will unite with those of the opposite kind, i.e., male with female. Sex among gametes may, then, be physiological, even where there is no observable morphological difference. Zoospores do not ordinarily unite with each other or with gametes. They develop new plants directly without the necessity of such union. Gametes as a rule must unite with other gametes or die. In exceptional cases unfertilized gametes produce new plants, and this process is called *parthenogenesis.* There is considerable evidence that in some algae the gametes evolved from zoospores.

In *Oedogonium,* in *Vaucheria,* and in most plants higher up in the scale of life there is not only a physiological but a morphological difference in gametes. Such are called *heterogametes.* In general, the male gametes are produced in great numbers and are small and actively motile, swimming to the female gametes, which are fewer, larger, less active, and usually without locomotion. In conjugation the male gamete contributes little except a nucleus. The female contributes a nucleus, an abundance of cytoplasm, and a supply of food for the early support of the new plant.

The advantages of differentiation in the size of gametes are quite apparent. (1) The large size of female gametes provides a greater supply of food for zygote and offspring. (2) The small size of male gametes increases the likelihood of gametic union (a) because of the fact that a parent cell of a given size will make a larger number of gametes if they are small, and (b) because of the fact that the small-sized gametes are more actively motile. To be sure, most of the male gametes are lost because there are not enough female gametes to conjugate with them, or because they fail to find them, but this loss is more than offset by the large proportion of the female gametes fertilized.

Economic Significance of the Chlorophyceae.—The Chlorophyceae, like the Cyanophyceae, are sometimes troublesome in water supplies. Those of both classes that grow on the surface of the soil or in superficial layers where light is available may decompose and add considerably to the supply of humus.

Relationships of the Chlorophyceae

The unicellular condition, the green color, the cilia, the cellulose walls, and the aquatic habit of the simpler Chlorophyceae suggest their relationship with the Flagellata, which are quite generally regarded as their ancestors. By a succession of evolutionary changes the filmentous Chlorophyceae such as *Ulothrix*, *Spirogyra*, and *Vaucheria* seem to have developed from the unicellular ones. The striking resemblance between *Chlamydomonas* and the zoospores of *Ulothrix* and some other filamentous Chlorophyceae seems rather significant.

There is evidence that the mosses and ferns had their ancestry in the green algae. The filamentous fungi, also, appear to have originated from algae, perhaps from the Chlorophyceae.

Phaeophyceae (Brown Algae)

The class Phaeophyceae is a moderately large one and rather distinct in its characters. The plants are almost exclusively marine and are the most conspicuous of the "seaweeds." They are especially abundant in the colder waters of the northern seas, particularly near the shore, where some of them cling to the rocks between high and low tide marks, a situation in which they are exposed to the air a part of the time.

The brown algae are so called because of the brown pigment, *fucoxanthin*, which occurs in the plastids along with the chlorophyll, giving them a golden-brown color. The nuclei are well developed, one to each cell. The differentiation into vegetative and reproductive portions is much greater in the Phaeophyceae than in the Chlorophyceae. The simpler forms, which are usually attached to rocks, are filamentous and much branched. The larger forms have the most highly specialized thallus found among the algae. In the giant kelps, for example, there is a large holdfast, a long stalk several inches in diameter, and a series of expanded branches, the whole effect crudely resembling root, stem, and leaves. There is no well-developed fibrovascular system, however, and none is needed in these plants, since they are wholly or partly sub-

merged. Some of these giant kelps are of very great length. There are measured specimens 150 feet long. Exceptional individuals have been reported to be more than an eighth of a mile in length, but such reports need verification.

Ectocarpus

This plant is chosen as a representative of the smaller filamentous brown algae. The thallus is a few inches long and much branched.

FIG. 170. Giant kelp, *Macrocystis*, one of the largest of the brown algae. (Reprinted by permission from Martin's *Botany, with Agricultural Applications*, John Wiley & Sons, Inc.)

It is found commonly along the seashore where it is exposed at low tide.

Asexual Reproduction.—*Ectocarpus* has two kinds of reproduction in its life history, but these are carried on by different plants, i.e., certain plants reproduce asexually and others sexually. In asexual reproduction, which occurs mostly in the winter, sporangia are formed in the tips of certain branches. In these sporangia numerous zoospores are produced. These are naked, oval cells, each having a nucleus, a golden-brown plastid, a red pigment spot, and two cilia which are attached at the side. After a brief period of swimming they settle down on some convenient object, attach themselves, and grow directly into new plants which look like their parent but are different in that they produce gametes instead of spores.

Sexual Reproduction.—The plants that grow from the zoospores are similar in appearance to the asexual ones, but they produce gametes instead of spores. They develop chiefly in the summertime and reproduce toward the close of the season. The gametes are formed in large

cells, *gametangia,* at the tips of the branches. The gametangia are much longer than the sporangia and are pointed at the tips. When mature, they are partitioned into many cubical cells, each of which pro-

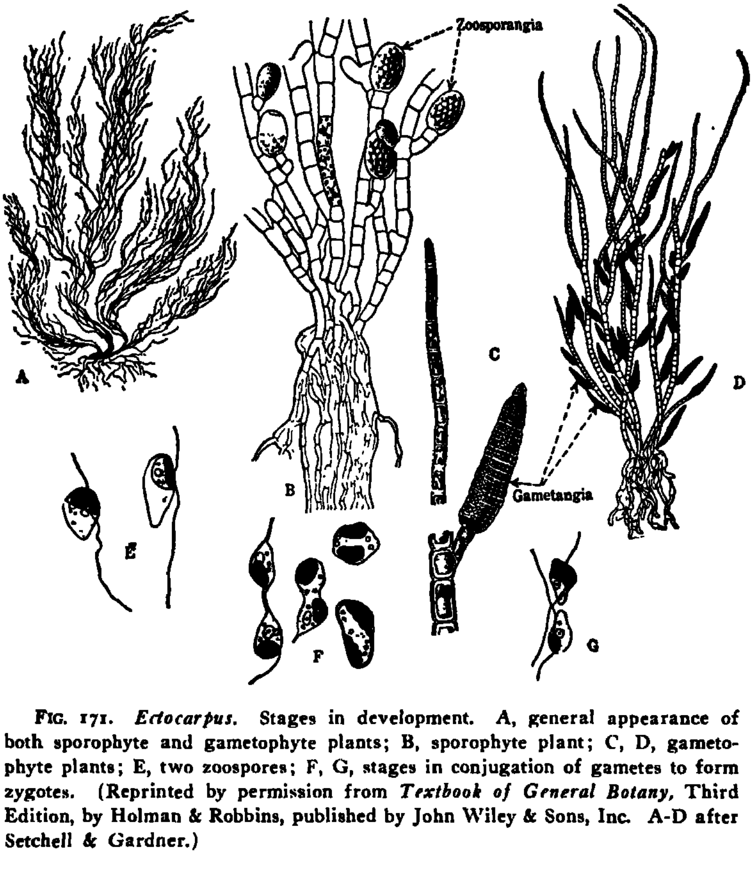


FIG. 171. *Ectocarpus.* Stages in development. A, general appearance of both sporophyte and gametophyte plants; B, sporophyte plant; C, D, gametophyte plants; E, two zoospores; F, G, stages in conjugation of gametes to form zygotes. (Reprinted by permission from *Textbook of General Botany,* Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc. A-D after Setchell & Gardner.)

duces a gamete. In some species the gametes are morphologically alike, i.e., of the same size and appearance. In others there is more or less difference in size, distinguishing them as male and female. Both kinds are much like zoospores in appearance and swim freely in the water. Under experimental conditions it has been observed that the female gametes are released from the gametangia in the morning, swim at once

to a region where the light is strong, and come to rest, attaching themselves to any convenient object. Soon the male gametes are released and hurry after them, spin about them for a few moments, clinging by the longer of the two flagella, and then one conjugates with each. If there are more males than females the less fortunate ones swim away as soon as the females have all conjugated. Gametes that fail

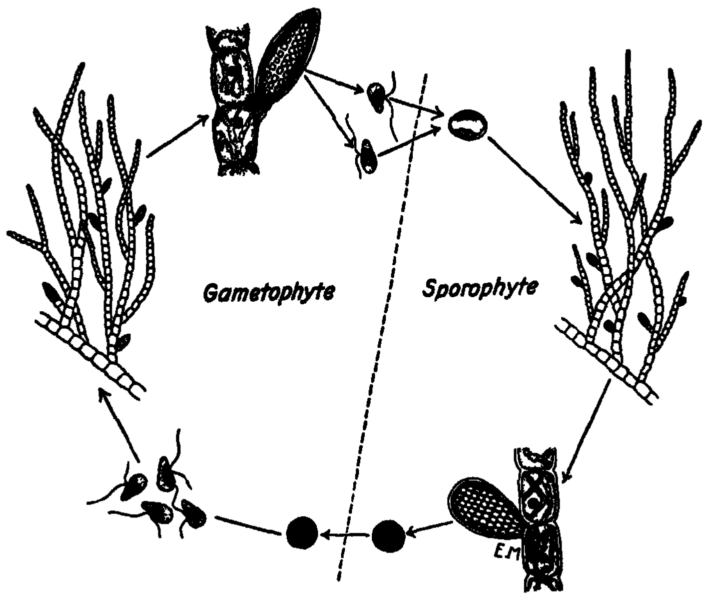


FIG. 172. *Ectocarpus*, life history.

to unite sometimes grow directly into new plants, presumably of the kind that produce sex organs, indicating that in this genus the difference between zoospores and gametes is not great. This parthenogenetic development is not uncommon among the lower plants and animals.

Life History.—In writing out the life history of this alga one immediately discovers an interesting phenomenon, namely, that spores and gametes are not produced on the same plant, but spore-producing, or asexual, plants alternate with gamete-producing, or sexual plants. This is in contrast with the condition found in *Ulothrix*, for example, in which cells of the same thallus produce zoospores and zoogametes in-

discriminately. This phenomenon is called an *alternation of generations.* A spore-producing plant or generation is called a *sporophyte* and alternates with a gamete-producing plant or generation, the *gametophyte.* A fundamental and important distinction between these two generations

FIG. 173. *Fucus* plant showing dichotomous branching. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc. After Oltmans.)

is that in the sporophyte plant each nucleus has *twice* the number of chromosomes found in the nuclei of the gametophyte plant. The explanation is simple. When the gamete nuclei fuse, the male and female chromosomes remain distinct, thus doubling the chromosome number. The zygote, with its double, or *diploid,* chromosome number, grows into the sporophyte generation in which each nucleus is diploid. In the formation of spores from the spore mother cells chromosome conjugation occurs, and the resulting spores have the single or *haploid*

chromosome number. The spore germinates and grows into the gametophyte generation, which is likewise haploid and forms haploid gametes.

This alternation of generations should be clearly understood, for it occurs in many Thallophytes and in all plants above the Thallophytes.

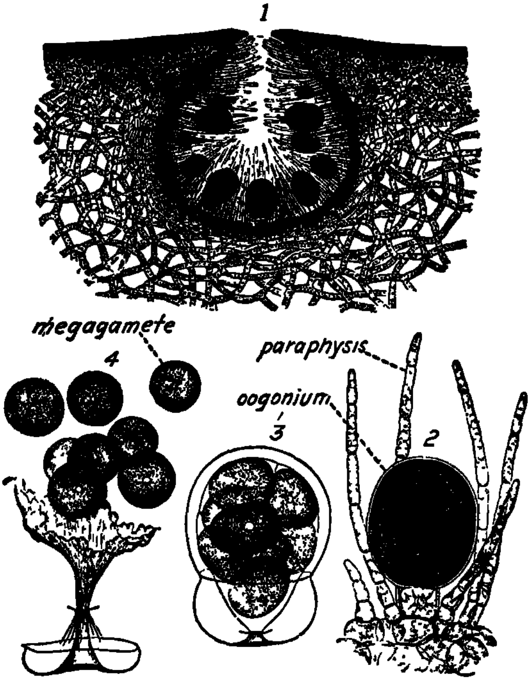


FIG. 174. *Fucus*, female reproductive parts. 1, section through female conceptacle containing oogonia; 2, 3, oogonia containing female gametes; 4, oogonium breaking and releasing gametes. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Thuret.)

It fails to occur only where gametic union is followed promptly by chromosome conjugation, thus eliminating the sporophyte generation.

Fucus

One of the commonest of the "rock weeds" of the beach, between tides, is *Fucus*. This plant is representative of the larger types of brown algae, although it is by no means the largest.

Vegetative Structure.—The thallus is a few inches in length, thick, stout, and leathery in texture. It is flat, with a thick midrib running lengthwise through the center. There are found at intervals hollow bladders filled with carbon dioxide mixed with other gases. These

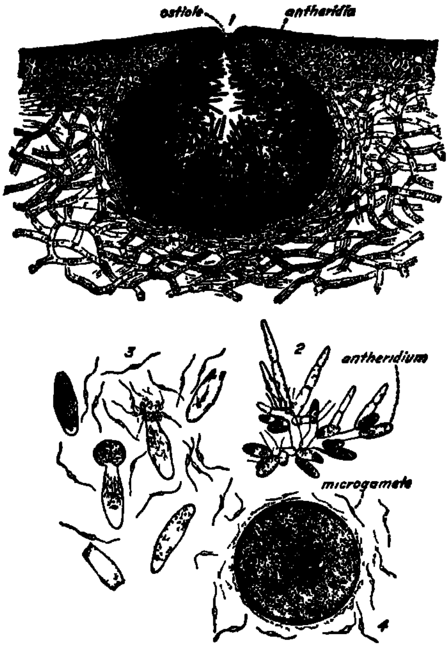


FIG. 175. *Fucus*, male reproductive parts. 1, section through male conceptacle containing antheridia; 2, antheridia containing male gametes; 3, male gametes escaping from antheridia; 4, male gametes around female gamete. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Thuret.)

serve as floats and help to keep the plant erect when submerged. The branching is *dichotomous* in character, i.e., each branch forks at its tip into two that normally are equal in size.

Reproduction.—Asexual reproduction is not known to occur in *Fucus*. The tips of certain branches are specialized for gamete formation. In these conical tips are numerous cavities, *conceptacles*, within which are borne oogonia or antheridia or, in some species, a combination of the two.

Each female conceptacle bears several oogonia, which are nearly spherical and produce eight, large, non-motile egg cells each. These are discharged into the cavity of the conceptacle.

Each male conceptacle is lined with a mass of branching filaments bearing numerous antheridia. The antheridia are elongated sacs containing large numbers of antherozoids. The antherozoids are motile by means of two lateral cilia, one of which is longer than the other. If the plants are continuously submerged, both kinds of gametes drift out through the openings of their conceptacles. If they are allowed to dry by the receding tide, the gametes are forced out by shrinkage of the plant, sometimes whole antheridia and oogonia being extruded. After they are freed from the antheridia, the antherozoids are attracted to the egg cells, often in large numbers. The longer cilium of each attaches itself to the egg cell while the shorter one continues to lash the water. Suddenly one antherozoid penetrates the egg cell and fertilizes it, and the others swim away.

The zygote germinates without a period of rest. In doing so it enlarges, becomes multicellular, sends down a holdfast, and develops into a full-sized plant again. Unfertilized egg cells are sometimes known to develop parthenogenetically.

Relationships of the Phaeophyceae

There seems to be no direct connection between the Chlorophyceae and the Phaeophyceae. There is evidence that both evolved from the Flagellata (see page 394). No class of plants seems to have come from the Phaeophyceae.

Economic Significance

In certain places along the seashore brown algae are thrown up on the beach in enormous quantities. Some are used as a source of potash, and some are hauled away for fertilizer. Certain species extract iodine from the sea water, where it occurs in minute traces, and store it in their cells. A part of the iodine of commerce is obtained from these seaweeds.

Diatomaceae (Diatoms)

The diatoms are regarded by some botanists as a family of the Chlorophyceae and by others as a family of the Phaeophyceae, while still others treat them as a small independent class. More evidence is needed to determine the relationships conclusively.

Diatoms are very common in both salt and fresh water and on objects of all kinds that are subject to constant wetting. There are

hundreds of species, most of them distinctly unicellular but others colonial in the form of ribbons or attached by stalks to each other and to the substratum. They are without cilia, but many species have a gliding motion unlike that of most motile cells.

The cell structure is quite distinctive. There are two plastids, greenish-brown in color. The cell wall is impregnated with silica and has thick and thin areas in the form of beautiful sculpturing. This

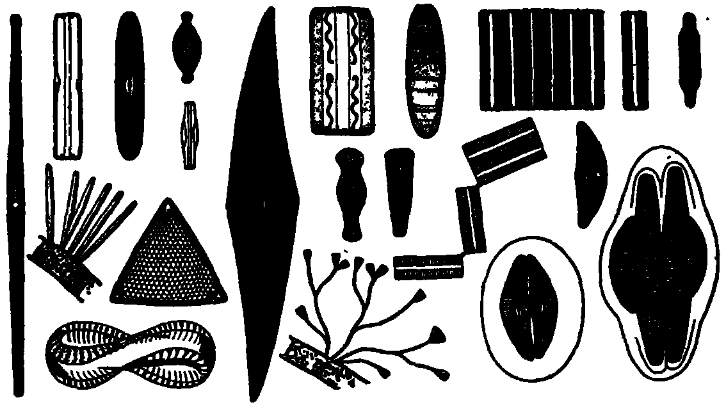


FIG. 176. Collection of diatoms showing variation in appearance. (From Kerner's *Natural History of Plants*, Blackie & Son.)

stony wall has the shape of a box with an overlapping cover. In cell division the cover rises and the cell divides longitudinally, one daughter cell receiving the box and the other the cover. Each then uses its portion for a cover and builds a box to fit inside it.

In addition to this reproduction by simple cell division, conjugation occurs at intervals. In some species each protoplast becomes a single gamete. In others it divides to form two gametes or possibly more. The zygote formed by conjugation becomes a single diatom which builds for itself a new box-like shell.

The siliceous shells of diatoms are very durable, and in many places they have formed deposits in the earth's crust several feet in thickness. This "siliceous earth," or "diatomaceous earth," has considerable value for making grinding powders that are less hard than emery and carborundum. It is also used for the construction of bacteriological filters and in the manufacture of certain kinds of dynamite.

Rhodophyceae (Red Algae)

The Rhodophyceae, like the Phaeophyceae, are mostly marine algae, although a few species are found in fresh water. They are most common in the warmer waters of the ocean and some of them are found farther out from the shore, in deeper waters than are the green and the brown algae.

The Rhodophyceae are mostly small, branching, filamentous plants with a basal attachment. In a few genera the thallus is broad and flat. The color is usually light red but varies from yellowish or pink to dark purple or purplish brown. Red algae are the most beautiful plants that live in the sea. The color is due in part to the presence of a pigment, *phycoerythrin,* along with chlorophyll in the plastids. This pigment probably aids in carbohydrate formation in deep waters where the intensity of light, especially that of the longer wave lengths—the yellow and red—is greatly reduced. True starch is not formed, but in its place appears a similar carbohydrate. Protoplasmic strands may be seen extending through the walls of adjacent cells. No ciliate condition is found in the Rhodophyceae at any stage of development. Both asexual spores and gametes are non-motile.

Nemalion

One of the simplest of the Rhodophyceae is *Nemalion.* It grows abundantly along the seashore at about the low tide mark.

Vegetative Structure.—*Nemalion* is a foot or less in height and consists of coarse, much-branched, slimy strands, each more than one cell in diameter. The color is light red or pink, and the plants, waving in shallow water, are beautiful in appearance. They are too weak to stand alone when the tide is out and they are not supported by the water.

Reproduction.—Both male and female organs are borne on the same plant. The male portions consist of dense tufts of short branches, each bearing a *spermatium,* or male gamete, at the tip. The female portions consist of fewer branches, each ending in a *carpogonium.* This is a female cell having a swollen base containing an egg nucleus and bearing a long hair-like extension, the *trichogyne.*

The spermatia are released in large numbers, and, being non-motile, are dependent on currents in the water to carry some of them to the trichogynes. Those which, by good fortune, come in contact with a

trichogyne, attach themselves to it, and the process of fertilization begins. An opening forms at the point of contact, and the protoplast of a spermatium enters the trichogyne. As it progresses downward to the carpogonium the nucleus divides, and one of the resulting nuclei unites with the egg nucleus. The zygote then undergoes nuclear and cell division until a mass of short branches is formed from it. The tip

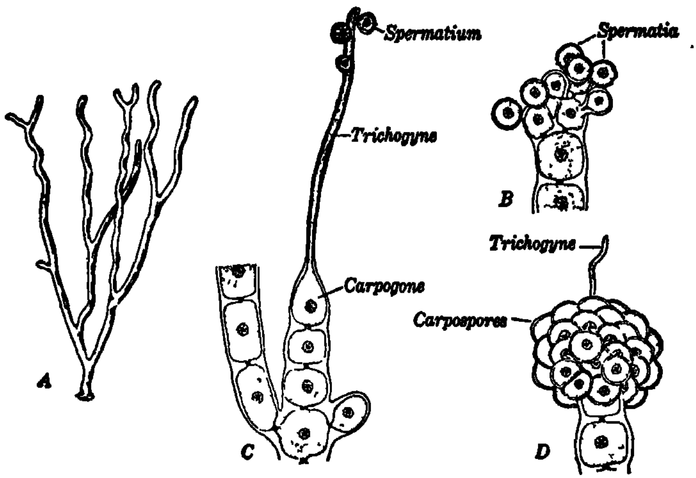


FIG. 177. *Nemalion.* Stages in development A, entire plant; B, tip of a branch bearing spermatia; C, tip of a branch bearing a carpogonium; D, cluster of carpospores produced by the zygote. (From Smith, Overton, et al., *Textbook of General Botany,* The Macmillan Company.)

cell of each branch becomes a *carpospore,* and a dense cluster of them results from each conjugation. It is noteworthy that each carpospore has received the benefits of the recent conjugation process. When mature they are released and grow into new plants.

Polysiphonia violacea

Polysiphonia violacea is representative of the more highly developed Rhodophyceae. This plant is deep red in color and is common in the ocean some distance out from shore. The main stalk consists of a central core of cells, surrounded by a cellular sheath closely adhering to it. This main stalk branches, and these larger branches in turn give rise to others that are only one cell in thickness. Thus the plant is given a very bushy appearance.

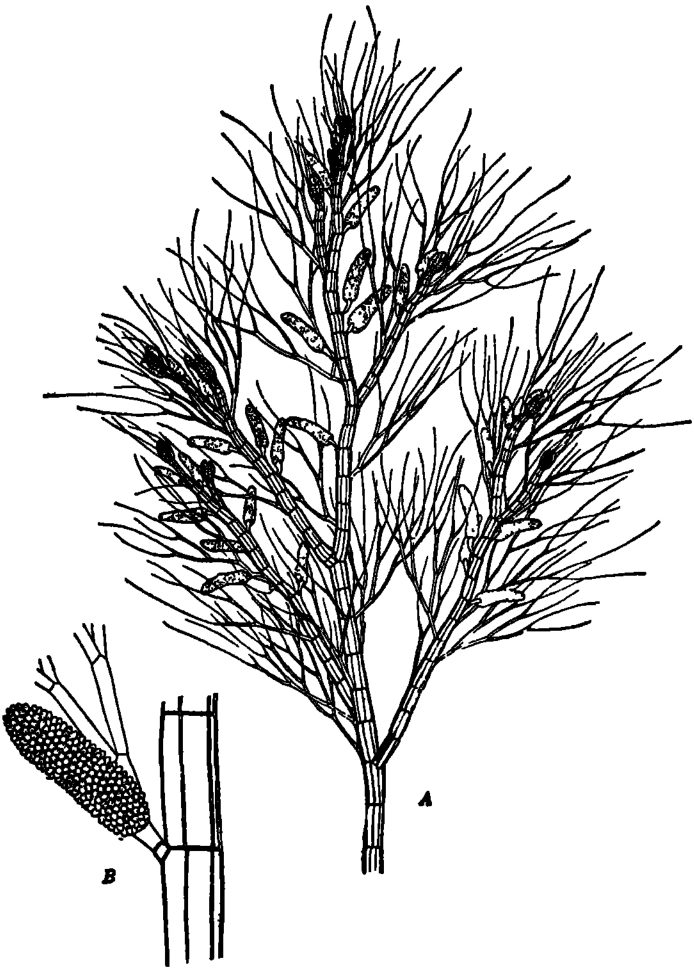


FIG. 178. *Polysiphonia.* A, portion of plant with spermatia; B, cluster of spermatia. (From Smith, Overton, et al., *Textbook of General Botany*, The Macmillan Company. After Thuret.)

Asexual Reproduction.—In *Polysiphonia violacea* certain plants produce asexual spores but no gametes. The spores are produced in groups of four by the division of the protoplasm of the sporangium. They are, therefore, called *tetraspores*. They grow into plants of similar appearance that produce gametes but not tetraspores.

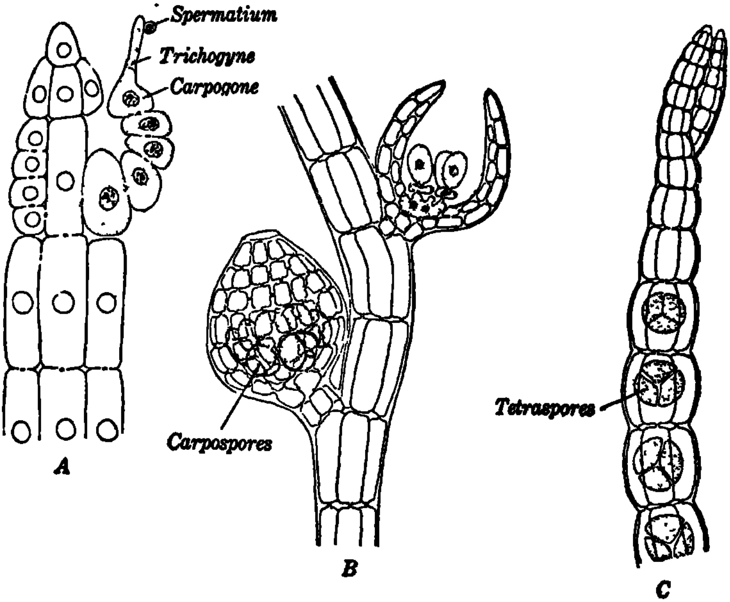


FIG. 179. *Polysiphonia*. A, carpogonial branch; B, external and sectional views of sheath enclosing carpospores; C, branch of sporophytic plant bearing tetraspores. (From Smith, Overton, et al., *Textbook of General Botany*, The Macmillan Company.)

Sexual Reproduction.—From the tetraspores grow male plants that bear spermatia and female plants that bear carpogonia with trichogynes. It is supposed that two of the tetraspores produce male plants and the other two produce female plants. On the male plants the spermatia are massed in dense clusters on short, stout branches; on the female plants the carpogonia are the tip cells of isolated five-celled branches.

A male gamete, or spermatium, after being released and coming in contact with a trichogyne, sends its nucleus, without division, down through it to the egg nucleus with which it unites. In the meantime, cells of the branch bearing the carpogonium have divided to form a

considerable number of *auxiliary* cells. A passage is then made from the carpogonium through an auxiliary cell into the basal cell of the branch, and through this opening the zygote nucleus passes into the basal cell. Meanwhile, the auxiliary cells have united with the basal cell to form a large, complicated, nutritive chamber for the reception of the zygote nucleus. From the auxiliary cells this chamber has re-

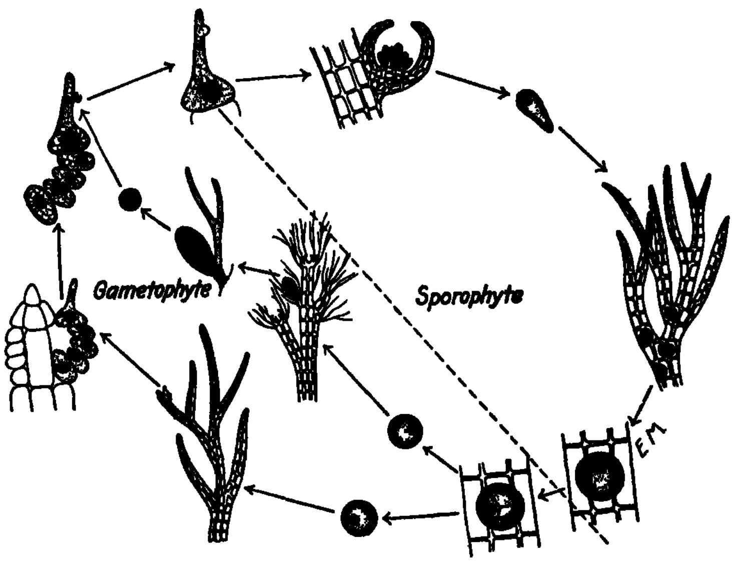


FIG. 180. *Polysiphonia,* life history.

ceived a supply of food for the rapid development that now takes place. As soon as the nutritive chamber has received the zygote nucleus, it sends out several branches which produce carpospores, each provided with a nucleus descended directly from the conjugate nucleus. These carpospores are enclosed by a layer of protective cells that forms an urn-shaped structure, from which they escape to form plants that reproduce by asexual tetraspores. The carpospores serve as amplifiers to the zygote. Alone it could produce but one sporophyte plant. Through the carpospores, however, it can produce many such plants.

Life History.—*Polysiphonia violacea* is a red alga with a distinct alternation of generations. Male and female gametes are borne on separate gametophyte plants in which the nuclei have 20 chromosomes.

Following conjugation the zygote undergoes a development that results in many carpospores that have 40 chromosomes. They in turn form sporophyte plants which have nuclei with 40 chromosomes, but which bear tetraspores in which the chromosome number has been reduced to 20. In each life cycle three plants are found: (1) male gametophytic plants, (2) female gametophytic plants, and (3) sporophytic plants. All three look essentially alike but differ in their reproductive bodies. Two kinds of spores are produced. Tetraspores, with haploid nuclei, on the sporophyte plants, and carpospores, with diploid nuclei, that originate by cell division of the zygotes still attached to the female gametophyte.

Relationships

The Rhodophyceae constitute a clear-cut and distinctive class. The presence of phycoerythrin, the lack of true starch, the cytoplasmic connections between cells, and the lack of any motile stage form a complex of characters quite different from that found in any other group. Their ancestry is quite unknown.

There is a theory that certain fungi, the Ascomycetes and possibly also the Basidiomycetes (Chapter XX), evolved from the Rhodophyceae by acquiring a terrestrial habit and losing their pigments.

Economic Significance

In addition to furnishing food for marine animal life the red algae supply some materials useful to man. A few species are used quite extensively for food, not only by the Chinese and Japanese but by the people of northwestern Europe, Icelanders, Norwegians, Scotch, and Irish. Livestock, especially sheep, often feed on red algae left on the seashore by the receding tide. Some yield valuable gelatinous substances such as "Irish Moss" and agar-agar.

An Unappreciated Benefit

We do not need to be told that a considerable proportion of the animal life is in the sea. From this great storehouse man has been able to obtain a vast amount of food, chiefly fish. What do the fishes of the sea live upon? They do not eat algae to any great extent—the story is not so simple.

Most algae live out their term of life and die, but during life or after death they supply food for myriads of tiny animals of many kinds. These animals are preyed upon by others that are larger, and in this way

ultimately the algae become food for fishes. It is, then, an interesting speculation as to whether or not the marine plants support as much animal life as do the land plants. Man cannot secure for his use as large a proportion of marine animals as of land animals, but he gets enough to entitle the algae to greater recognition than they commonly receive.

Review Questions

1. Does the term "algae" have a place in the regular categories of botanical classification, and if so what is its rank?
2. To what *division* do the algae belong?
3. What characters do algae have in common?
4. Give the common names and the corresponding botanical names for the four classes of algae.
5. Where is each most commonly found?
6. How do plants generally differ from animals with reference to the following characters: (1) locomotion, (2) cell walls, (3) presence of chlorophyll, (4) nutrition?
7. Give the source of each of the following for submerged algae: (1) carbon, (2) oxygen, (3) minerals.
8. Why do not large seaweeds need a well-developed fibrovascular system?
9. Name a class of organisms on the border line between plants and animals.
10. What characters do all the members of the Flagellata have in common?
11. Give the generic and specific names of a flagellate with both plant and animal characters.
12. Describe the cell structure of *Oscillatoria*.
13. Compare blue-green algae and the bacteria: (1) with respect to nuclear structure, (2) with respect to reproduction, (3) with respect to nutrition.
14. State the evidence of a close relationship between blue-green algae and the bacteria.
15. Name four members of the Chlorophyceae that have been studied in this course.
16. Describe the appearance of the vegetative state of each.
17. Describe the asexual reproduction of *Ulothrix*.
18. Give the name of an alga that closely resembles a zoospore of *Ulothrix*.
19. Describe the structure of this alga.
20. Describe the sexual reproduction of *Ulothrix*.
21. What is the difference between a zoospore and a gamete of *Ulothrix*: (1) in morphology? (2) in physiology?
22. What is the distinction between isogametes and heterogametes?
23. What advantage is there to the plant in having large female gametes and small male gametes?

24 Define (1) pyrenoid, (2) coenocyte, (3) parthenogenesis, (4) filament, (5) sporangium
25 Why would you not expect to find *Spirogyra* in a flowing stream?
26 State two ways in which the Phaeophyceae differ in appearance from the Chlorophyceae
27 Name two examples of the Phaeophyceae
28 What is meant by the "alternation of generations"?
29 In *Ectocarpus* what two kinds of plants are produced?
30 What kinds of fruiting bodies does each produce?
31 From what kind of a reproductive body does each grow?
32 How does the chromosome number of the gametophyte compare with that of the sporophyte?
33 What stimulus causes the male gametes of *Ectocarpus* to swim toward the female gametes?
34 After one male gamete conjugates with a female gamete, what causes the others to leave?
35 Write out the full life history of *Ectocarpus*
36 Describe the reproduction of *Fucus*
37 Of the four classes of algae, which grow in the deepest water? Why?
38 Which light rays penetrate water most readily?
39 What is the product of photosynthesis in the Rhodophyceae?
40 Name two examples of the Rhodophyceae
41 Describe the reproduction of *Nemalion*
42 How many kinds of plants are found in *Polysiphonia*?
43 What kind of reproductive body does each produce?
44 From what kind of reproductive body does each grow?
45 What is the difference between the method of tetraspore formation and that of carpospore formation?
46 Write out the full life history of *Polysiphonia*
47 Define (1) spermatium, (2) diatom, (3) carpogonium, (4) trichogyne, (5) auxiliary cell
48 Give the functions of each of the following (1) pyrenoids, (2) antheridia (3) antherozoids, (4) oogonia (5) auxiliary cells, (6) trichogyne
49 Which of the four classes of algae have a motile condition and which do not?
50 What is the difference between conjugation and fertilization?
51 Give singular and plural forms of each of the following (1) antheridia (2) alga, (3) nuclei, (4) sporangium, (5) cilia, (6) oogonia
52 Give the economic significance of the Rhodophyceae, of the Phaeophyceae
53 In what ways are algae harmful to man?
54. What is the greatest economic value of algae to man?

CHAPTER XX

THALLOPHYTA—FUNGI

There are vast numbers of plants, literally thousands of species, that have a simple filamentous structure and are without chlorophyll. These are the *fungi*.[1]

Almost without exception plants belonging to the fungi have reproductive parts distinct from the vegetative part, or plant body, which is not true of the bacteria and other one-celled organisms. The body of a fungus consists of a very much-branched, thread-like mass, the *mycelium,* each branch of which is a *hypha;* or to express it in another way, the entire collection of branching hyphae makes up the plant body or mycelium. As the plant approaches maturity it reproduces by asexual spores formed either at the tips of certain hyphae by constriction, or within a sporangium by cleavage. Most fungi have sexual reproduction also.

PHYCOMYCETES

This class of fungi is so named because it shows some similarity to certain members of the Chlorophyceae, although the chlorophyll is lacking. It is a relatively small class with but 1300 species. A few of them are found in ponds, streams, ditches, and very wet soil; others on the land everywhere, particularly on decaying vegetation; and a considerable number are parasitic on plants.

The character that all these species have in common, one which suggests a relationship that brings them into one class, is the structure of the mycelium. The mycelium of the Phycomycetes is *non-septate,* i.e., it is without cross-walls dividing it into cells, with the exception of the

[1] There is a difference in usage with regard to the common name "fungi." Some use this term as defined above and others use it to include all or practically all of the Thallophyta that are without chlorophyll, even though admitting that the bacteria and the slime molds are not closely related to each other nor to the three classes described in this chapter. Such a practice tends to give a false impression of relationship and makes necessary the use of such terms as "true fungi" or "filamentous fungi" for these three classes.

walls that form in the process of reproduction. This condition is in contrast with that found in other classes of fungi that have cross-walls at frequent intervals. It is similar to that found in *Vaucheria,* and these fungi, like *Vaucheria,* are called coenocytes.

Rhizopus nigricans

There are two sub-classes of the Phycomycetes. One of these, the Zygomycetes, is represented by the common bread mold, *Rhizopus*

FIG. 181. *Rhizopus.* Culture growing on bread in a covered dish.

nigricans. This fungus is common on all sorts of decaying materials and even attacks ripe fruits and vegetables. Its spores, which are distributed by the wind, are so abundant that if a piece of moist bread is exposed for a half hour to the air of almost any room a growth of it will be obtained.

Vegetative Structure.—In most respects the thallus of *Rhizopus* is representative of the fungi. It consists of a much-branched, thread-like mass called the mycelium, which forms a loose, fluffy mass several inches in diameter. The mycelium develops within the substratum (bread, for example) from which it absorbs food. As the plant grows it sends out aerial branches called *stolons,* which extend the plant as do the "runners" of the strawberry. These stolons attach themselves at in-

tervals to the substratum by means of special hyphae known as *rhizoids,* which serve for anchorage and may absorb a little food. At this stage the plant appears as a conspicuous, cottony mass, white in color when young but turning dark with age.

When studied closely with the microscope the mycelium is seen to have practically no cross-walls, or *septa,* and the plant is a coenocyte with hundreds of nuclei. These nuclei are well developed but tiny and

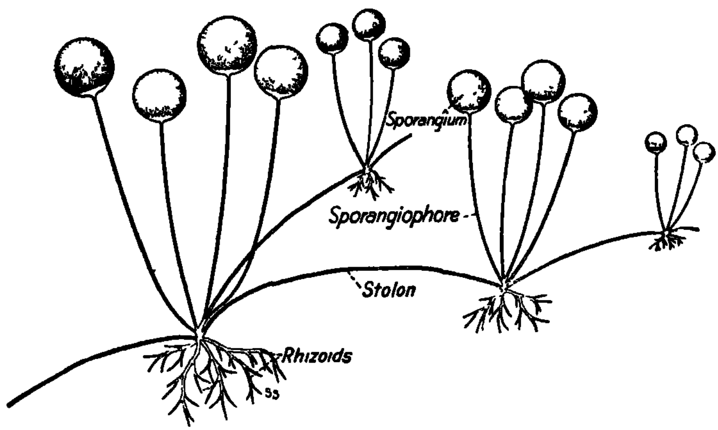


FIG. 182. *Rhizopus.* Plant spreading by stolons and bearing sporangia on sporangiophores.

so transparent that they cannot be distinguished in living, unstained plants. The protoplasm can often be seen streaming through the hyphae for long distances.

Asexual Reproduction.—At certain intervals on the aerial part of the mycelium, where the rhizoids are sent out by the stolons, groups of vigorous *sporangiophores* grow upward. The tip of each sporangiophore swells to form a *sporangium* which will later produce spores. Cytoplasm, bearing many nuclei, streams up the sporangiophore and into the sporangium, forming, toward the outside, a dense layer which surrounds a much-vacuolated central portion. Near the boundary between the dense and the vacuolated cytoplasm there forms a definite layer of small vacuoles. These become flattened, unite with each other, and, aided by a surface cleavage furrow at the base of the sporangium, separate the central *columella* from the outer protoplasmic layer, which is then divided into many spores by numerous cleavage furrows. Each

spore contains several nuclei and secretes a wall around itself. Finally the wall of the sporangium becomes ruptured, allowing the spores to escape and be distributed by the wind. These spores are non-motile and

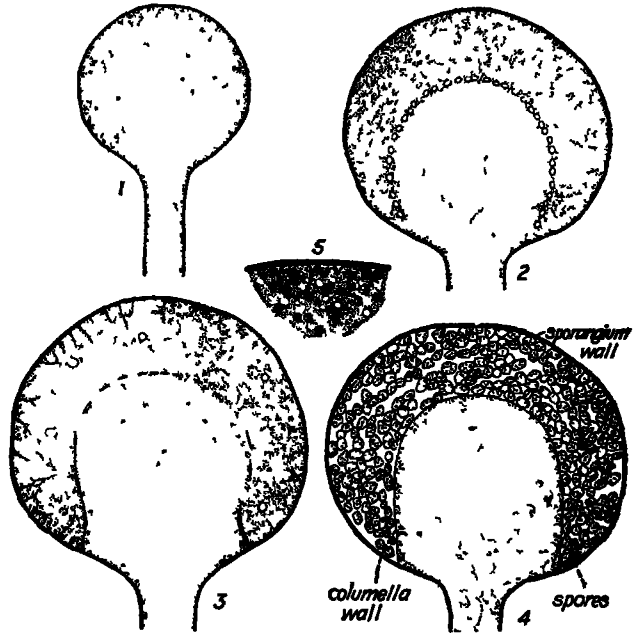


FIG 183 *Rhizopus* Stages in spore formation 1, sporangiophore bearing a young sporangium 2 3 columella being separated from the spore forming protoplasm by vacuoles 3 spores forming by cleavage furrows, 4 sporangium full of spores, 5, highly magnified portion of a sporangium showing cleavage furrows cutting between nuclei and vacuoles

under favorable conditions each is capable of developing into a new plant

The method by which spores produce new plants is very simple. A spore absorbs moisture and swells considerably, then at one point, or sometimes two, the wall softens and internal pressure forces out a germ tube This germ tube grows and branches until an extensive mycelium is formed, which later produces reproductive bodies.

Sexual Reproduction.—A single plant of this fungus cannot carry on sexual reproduction alone, in fact, two plants cannot do so if they

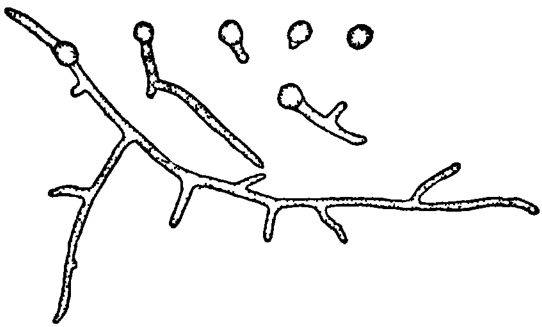


FIG. 184 *Rhizopus* Spores germinating and forming a mycelium

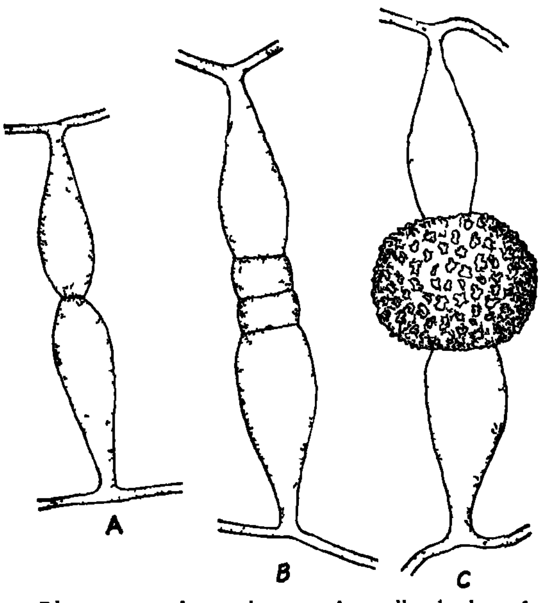


FIG. 185 *Rhizopus*, sexual reproduction A, swollen hyphae of + and — strains preparatory to gamete formation, B, gametes ready to conjugate; C, zygospore and suspensors

are exactly alike. It has been shown that in *Rhizopus nigricans,* as in some of its relatives, there are two strains. The terms *plus* and *minus*

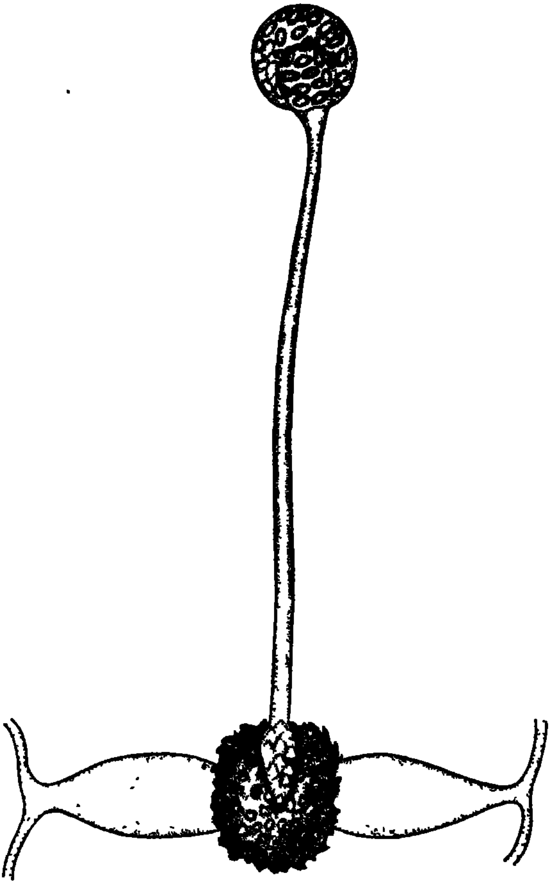


FIG. 186. *Mucor,* a fungus closely related to *Rhizopus.* Sporophyte formed by germination of zygospore.

are applied to these, although they might have been called male and female. They look practically alike except that the plus strain is a little more vigorous in its growth. If a plant of a plus strain and one of a minus strain are growing close together so that the advancing hyphae reach each other, conjugation takes place. During this process

the hyphae become club-shaped and develop multinucleate gametes at their tips by the formation of cross-walls. Two gametes from plants of opposite strains become pressed tightly together, and the abutting walls dissolve, allowing the protoplasm to mingle and the nuclei to fuse—probably in pairs. A heavy, rough, dark wall now forms and the body is called a *zygospore*.[1] It is held for a time by the two *gametophores*, which at this stage are termed *suspensors*. They are the remains of the hyphae from which the gametes were produced.

After a period of dormancy the zygospore germinates by sending out a dwarf mycelium bearing one or two sporangiophores, each of which bears at its tip a tiny sporangium in which asexual spores are borne. It is presumed that some of these spores produce plants of the plus strain and others from the same sporangium produce plants of the minus strain. In practice it has been found very difficult to induce the zygospores to germinate. This suggests the likelihood that in nature new plants come almost entirely from asexual spores and that the zygospores usually die without aiding in reproduction. It is customary to regard the main plant which produces stolons and bears both sporangial spores and gametes as the gametophyte generation and the dwarf mycelium growing from the zygospore and producing sporangial spores as the sporophyte generation, but the chromosome numbers of these structures have not been determined.

Rhizopus belongs to the family Mucoraceae, which contains other genera in which one plant produces both male and female gametes. Such plants are *homothallic* while *Rhizopus*, requiring two physiologically different strains for zygospore formation, is *heterothallic*.

Saprolegnia

The second sub-class of the Phycomycetes is the Oomycetes, represented by *Saprolegnia* and *Phytophthora*.

Saprolegnia is one of the "water molds," so called because they live in water, whereas most other fungi live on a solid substratum exposed to the air and are unable to reproduce if kept submerged. *Saprolegnia* grows commonly in surface water or in wet soil. It lives chiefly on vegetable matter and the bodies of dead insects, but some species are parasitic on fishes. The spores are discharged into the water in great abundance. If pieces of apple or the fruits of the hawthorn or rose

[1] Resting zygotes formed by the union of equal-sized gametes are called *zygospores*. Those formed by the union of small male gametes with large female gametes are called *oospores*.

are suspended in pools, ditches, or streams, they are likely to be attacked by *Saprolegnia* or related fungi, which will penetrate them and later grow in the form of a conspicuous, soft, downy mass consisting chiefly of a non-septate mycelium.

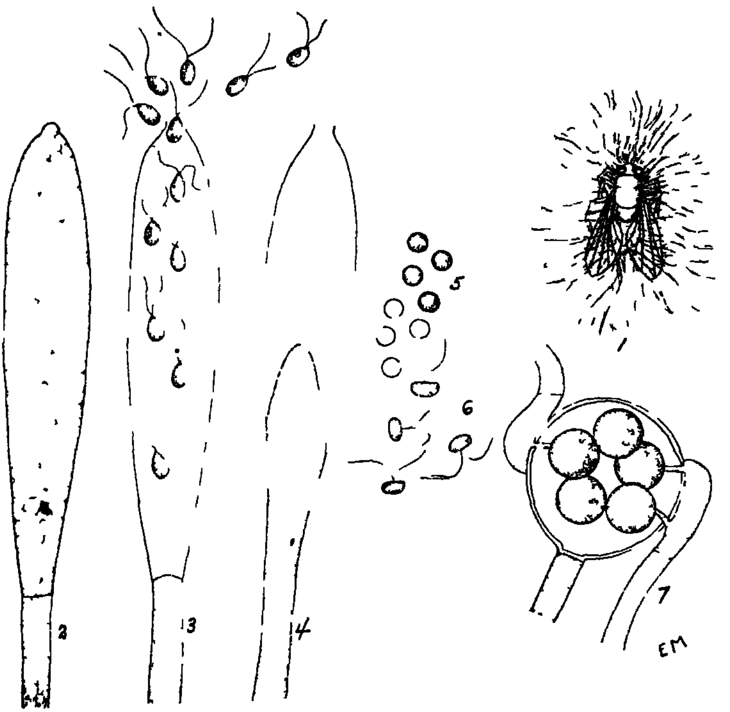


FIG. 187. *Saprolegnia* Stages in development. 1, fungus growing on a dead fly in water; 2, sporangium with newly formed spores; 3, sporangium discharging zoospores; 4, formation of new sporangium; 5, resting stage following first motile stage 3; 6, second motile stage following resting stage 5; 7, fertilization of eggs in oogonium.

Asexual Reproduction.—The tips of the hyphae protruding from the substratum develop relatively large, club-shaped sporangia, separated from the vegetative hyphae by cross-walls. These sporangia, when young, have a central vacuole surrounded by a layer of protoplasm with many nuclei. Soon this protoplasm becomes divided by cleavage furrows from the central vacuole into pear-shaped zoospores, each having

two cilia at the small end. Each pair of cilia is attached to a tiny granule, or *blepharoplast,* just inside the plasma membrane, and this granule in turn is connected with the single nucleus. An opening forms in the tip of the sporangium and through this the zoospores escape. They are unable to develop at once into new plants. Instead, they withdraw their cilia, become spherical, and secrete walls about themselves. After a short time the protoplasts escape from their walls through tiny openings and again become active, but this time they are bean-shaped as a rule, with the two cilia issuing from the concave side. If these spores find suitable food materials they come to rest and germinate by producing tubes that penetrate the substratum, thus forming new plants.

Sexual Reproduction.—Shortly after the first sporangia have discharged their spores, oogonia and antheridia are produced on hyphae similar to those that produced sporangia. The oogonia are spherical, or nearly so, and their protoplasm contains many nuclei. Cross-walls now form through the stalks, separating the protoplasm of the oogonia from that of the mycelium. As each oogonium matures, its protoplasm is divided by cleavage into several egg cells. The antheridia are produced close to the oogonia on the same or neighboring hyphae. They are rather slender, only slightly larger than the hyphae that produce them. They press against the oogonial wall and each sends a tube through it to an egg cell. Through the fertilization tube one or more male nuclei pass into the egg cell. The zygote thus formed is an *oospore* that envelops itself in a thick wall.

Sometimes the antheridia fail to form or, although formed, fail to fertilize the egg cells. In such cases the egg cells often develop by parthenogenesis as though fertilized. Parthenogenesis occurs widely throughout the plant kingdom, but it is especially common in the Oomycetes.

After a period of rest the oospores germinate. This takes place, in some cases at least, by germ tubes growing out to form a mycelium. It should be mentioned, however, that in some of the Oomycetes the oospores germinate by the division of the protoplast into zoospores.

Phytophthora infestans

A considerable number of the Oomycetes are parasitic on higher plants. Those belonging to one family are called the "downy mildews" because of the conspicuous hyphae growing out from the stomata of the leaves and stems which they have attacked.

Occurrence.—*Phytophthora infestans* causes the late blight or downy mildew of potato, a very destructive disease, widespread throughout the northeastern United States, Europe, and some other parts of the world.

When zoospores of this fungus are deposited on the leaves or other parts of the potato plant, they germinate and the germ tubes attack the

FIG. 188. Left, potato plant blighted by an attack of *Phytophthora infestans*. Right, potato leaf showing infected areas. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Stewart.)

host plant either through the stomata or through the unbroken epidermis. Once inside, the fungus grows through the spaces between the cells as a non-septate mycelium. From this mycelium special branches, known as *haustoria*, penetrate the living cells of the potato plant and withdraw nourishment for the support of the parasite. These are very numerous. In its formation a haustorium branches from a hypha that runs through an intercellular space and lies in contact with a cell wall. A very tiny opening is formed through the wall through which the haustorial branch extends, swelling to a bulbous form inside. Here it lives in contact with the cytoplasm of the host from which it absorbs nourish-

ment for the parasite. Each haustorium contains a nucleus, a fact which suggests that the nucleus has a part to play in the absorption of food.

Many kinds of parasitic fungi obtain their food by means of haustoria, but others send undifferentiated hyphae into and through the cells of the host.

Reproduction.—Following this period of vegetative development the fungus reproduces asexually. Special hyphae, *conidiophores,* grow out

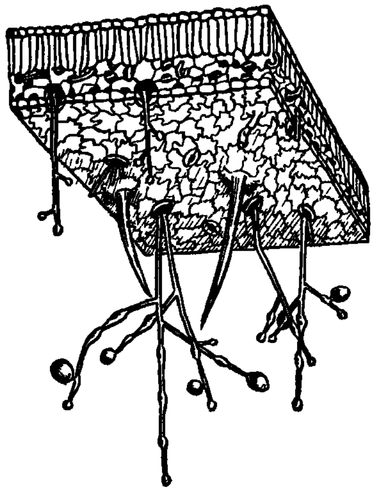


FIG. 189. Perspective view of potato leaf with conidiophores of *Phytophthora infestans* protruding from stomata and bearing conidia. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc. After Jones.)

through the stomata and then branch. On the tip of each branch an oval *conidium* is produced by constriction. The tip of the conidiophore continues to grow, pushing past the newly formed conidium, and produces another conidium and sometimes a third or even more.

These conidia germinate either on the fungus that bore them or after being blown or washed away. If there is abundant moisture and the temperature is moderately warm, the conidium sends out a germ tube, but if it is cool the conidium divides into zoospores. In the latter case the conidium becomes a *zoosporangium.* Most of the zoospores are lost through failure to find a suitable host plant, but those that are more fortunate attack other plants and thus spread the disease.

Phytophthora infestans does not ordinarily reproduce sexually. It was once supposed that this kind of reproduction had been lost by evolutionary degeneration, as is the case in many species of fungi belonging to the class Ascomycetes. It has been shown, however, that

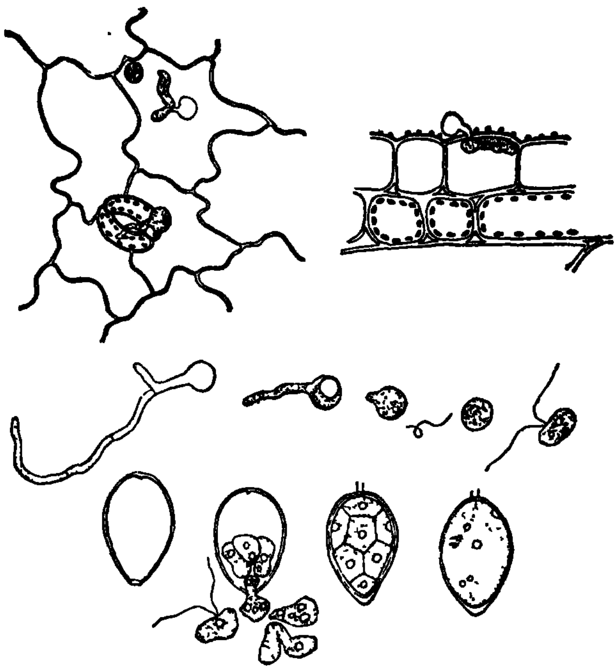


FIG. 190 *Phytophthora infestans.* Conidia germinating to form zoospores, and a zoospore germinating to form an infection thread. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Ward.)

certain other species of *Phytophthora* are heterothallic, the male form attacking one species of host plant and the female another. Under such circumstances the two forms have little chance of meeting. There is evidence that *Phytophthora infestans* is a female form, and in the presence of a suitable male it might produce oospores. The conidia and zoospores are short lived and do not survive the winter. The fungus is perpetuated in the potato tubers which it has attacked through the skin and has partly rotted.

One method for controlling fungus diseases of plants is well illus-

trated in this case. If the potato plants are sprayed with Bordeaux mixture, which contains copper hydroxide, the spores falling on them will be killed by the chemical as they germinate and no infection will occur. After the fungus has invaded the plant, however, the spray mixture cannot reach it, and it will continue to develop. Fortunately most parts of the United States have climatic conditions unfavorable to this disease, i.e., the temperature is either too high or too low for

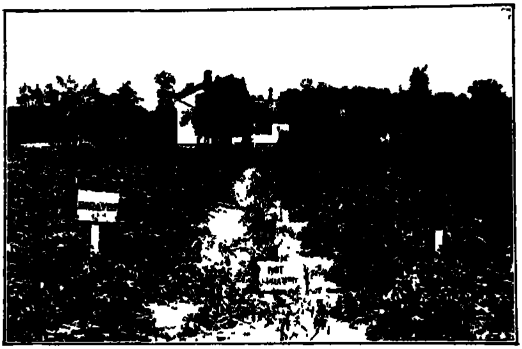


FIG. 191. Sprayed and unsprayed rows of potatoes in a field where late blight was prevalent. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Stewart.)

the fungus, or moisture is insufficient for the germination of the spores and their subsequent penetration of the potato plants.

Relationships of the Phycomycetes

It has long been held that the Phycomycetes originated as a result of the loss of chlorophyll by green algae. Whether all of this class came from the same algae or whether the Oomycetes and the Zygomycetes originated separately from different algae is debatable. There is much support for the latter view. Except for the non-septate condition of the mycelium there is little to bind these two groups into one class. The Zygomycetes have non-motile spores and gametes that are equal in size, or nearly so, while the Oomycetes form zoospores and have unequal gametes. Furthermore, in certain Oomycetes there is a layer of *periplasm* surrounding the eggs in the oogonia, which is lacking in the Zygomycetes. It is quite probable that each should be regarded as a class by itself, as is done by some authorities. Because of the similarity

existing between the motile stages in the Oomycetes and some of the Flagellata, *it seems not unlikely that the former evolved from the latter.*

Ascomycetes

The largest class of fungi is the Ascomycetes with nearly 38,000 species. Some of them are molds barely visible to the naked eye; others, such as the morels and the truffles, are fleshy fungi, one to several inches in diameter.

Occurrence.—These fungi are nearly all terrestrial and are of world-wide distribution. Wherever organic matter can be found, Ascomycetes also occur. Some species are saprophytes, others are parasites causing many of our most destructive plant diseases and a few animal diseases.

Vegetative Structure.—Unlike the Phycomycetes, the Ascomycetes have a septate mycelium, and in most species each cell has a single nucleus. The mycelium is usually whitish or transparent but is sometimes brown and occasionally highly colored—pink, red, yellow, green, or purple.

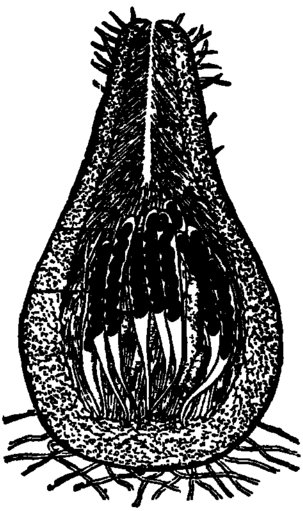


FIG. 192. Perithecium containing asci and ascospores. (From Sinnott's *Botany, Principles and Problems*, McGraw-Hill Book Company, Inc. After Tavel.)

Asexual Reproduction.—The predominating method of asexual reproduction is through the cutting off of conidia from the ends of conidiophores by constriction. Some species bear them in chains, others singly. In some cases a single plant bears hundreds of thousands of such spores. They are non-motile, and, indeed, the Ascomycetes as a class totally lack any motile condition.

Sexual Reproduction.—In certain of the species that have been closely studied, conjugation has been observed between gametes more or less unequal in size. From the zygote there develop one or more sacs called *asci*, in each of which are produced, by free cell formation, typically eight ascospores. In most orders of this class the asci are enclosed by a mass of mycelial branches, the *ascocarp*. This may form a firm

layer that entirely surrounds the asci, or it may have an opening at the top. Such an opening may be only a narrow pore through which the ascospores are later discharged, or it may be so wide that the ascocarp is cup-shaped or saucer-shaped. The term *perithecium* is applied to very tiny ascocarps that are either spherical and closed or flask-shaped with a small opening.

The tendency is for the conidia to spread the fungus rapidly during the summer, and for the ascospores or a dormant mycelium to carry it through the winter and give it a start in the spring.

Sphaerotheca humuli

The "powdery mildews" constitute a fairly large group of parasitic Ascomycetes, a few of which cause important diseases of economic plants. They are *strict* parasites, i.e., they are unable to develop without a host plant, in which respect they differ from many other fungi that may be parasitic if opportunity offers, or that may live a saprophytic life on dead plants or in artificial cultures in the laboratory. For the most part the mycelium is *external* to the host, making a weft over the surface, hence the term "surface mildews" frequently applied to them. Nourishment is obtained by means of haustoria that penetrate the epidermal cells of the host plant.

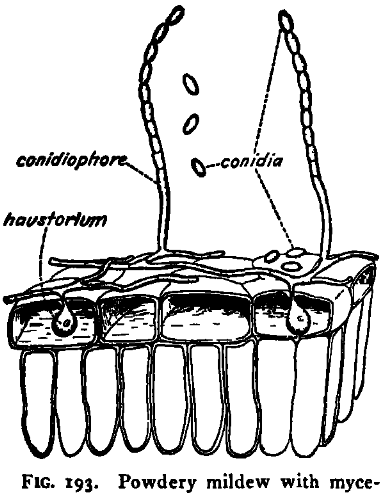


FIG. 193. Powdery mildew with mycelium on the surface of a leaf and haustoria in the epidermal cells. Asexual reproduction is by conidia. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

Vegetative Structure of Sphaerotheca — *Sphaerotheca humuli* is a mildew that is parasitic on the hop, dandelion, strawberry, and some other plants. Spores, germinating on the surface of the leaves, produce a whitish, septate mycelium that sends haustoria through the walls into the epidermal cells from which they absorb nourishment. Each haustorium contains a nucleus which apparently governs its activities.

Asexual Reproduction.—At numerous points the mycelium sends up conidiophores that produce conidia in chains, the terminal conidium of the chain being the oldest. These are formed in enormous numbers and have suggested the name "powdery mildew." They are responsible

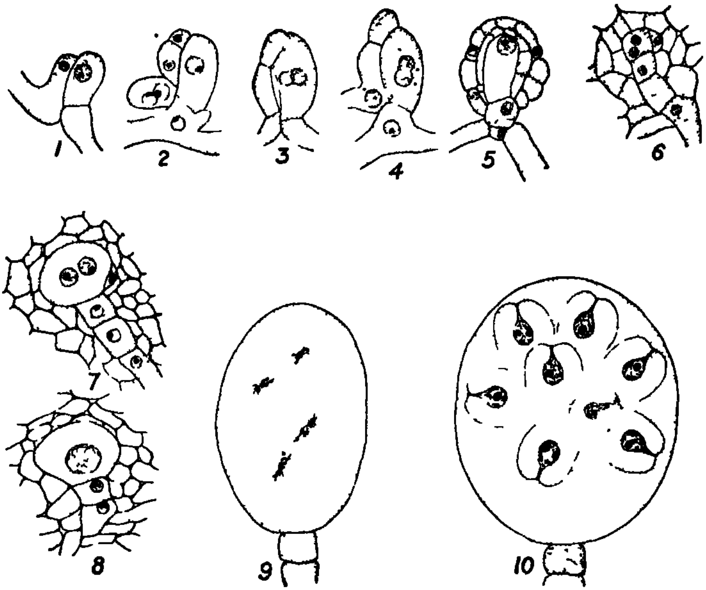


FIG. 194. *Sphaerotheca humuli*, sexual stages. 1 to 5, development of gametes and conjugation; 6, 7, formation of ascus from second cell from the tip of the ascogenous hypha; 8, nuclear fusion in the ascus; 9, nuclear division in the ascus; 10, spores being cut out by free cell formation. (1 to 8 redrawn from Harper.) 9 and 10 somewhat diagrammatic.

for most of the spread of the disease through the summer, but they are too delicate to survive the winter.

Sexual Reproduction.—After conidial formation has been going on for some time, sexual organs are produced. These consist of an antheridium and an oogonium that press closely together and sometimes twist about each other. Each contains a single nucleus. An opening dissolves through the wall between the antheridium and the oogonium, and the cytoplasm and nuclei of the two unite. The zygote nucleus then divides and the zygote develops a short row of cells. In the development of this hypha, nuclear division is somewhat more rapid than cell

division so that one, two, or three nuclei may be found in one cell. Ultimately cell walls are formed between these nuclei so that each cell is left with only one nucleus, with the exception of the one next the terminal cell which has two, probably not sister nuclei. This cell, second from the tip of the row, develops into an *ascus*. As it begins to enlarge, the two nuclei which it contains unite with each other. The ascus now grows rapidly, and its nucleus undergoes three successive divisions, thus

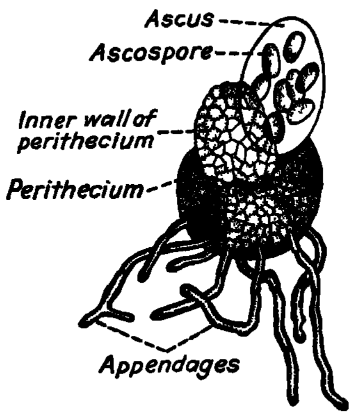


FIG. 195. *Sphaerotheca phytoptophila.* Perithecium with its single ascus and the inner wall crushed out. (Redrawn from Salmon.)

forming eight. Ascospores are formed about these nuclei by free cell formation. In this process each nucleus develops a beak with a star-shaped mass of fibers at the tip. These fibers fold down around the nucleus and the surrounding cytoplasm and thus cut out a uninucleate spore which then secretes a wall about itself. As all the nuclei of the ascus are included within the eight spores the remainder of the cytoplasm, the *epiplasm,* is left without nuclei. It is probable that the ripening spores absorb some nourishment from it.

In some other genera of Ascomycetes the zygote sends out several *ascogenous branches,* each of which forms an ascus, and in this way several asci containing many ascospores result from each gametic union.

While the ascus is developing, numerous hyphae originating below the zygote grow up around it in a compact mass to form a black, spherical, protective body, the *perithecium,* which is one form of ascocarp. It is barely visible to the unaided eye and protects the ascospores

over winter. In the spring the perithecium disintegrates, releasing the ascospores, some of which may be blown to host plants suitable for their attack.

The perithecia of the powdery mildews produce *appendages* which have branched, hooked, or straight tips according to the genus. Some of these are of remarkable appearance and considerable beauty if seen under the microscope. Their function is uncertain. One theory is that they

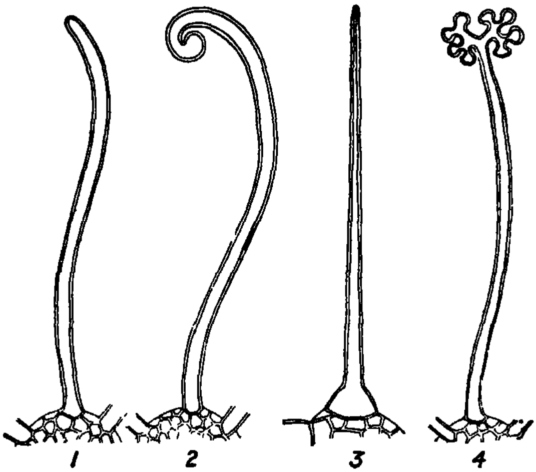


FIG. 196. Appendages on the perithecia of several mildews. 1, *Sphaerotheca;* 2, *Uncinula;* 3, *Phyllactinia;* 4, *Microsphaera.*

bend downward forcibly and thus lift the perithecium free from the surface to which it is attached. The shape of these appendages and the number of asci in each perithecium are among the characters used in classifying these fungi.

Sphaerotheca, which is representative of the powdery mildews, is homothallic, and this condition appears to be the predominant one among the Ascomycetes, but some heterothallic members of this class have been described.

Penicillium

One of the commonest of all the plants of the earth is *Penicillium,* of which there are several species. Most of the blue or green molds seen everywhere on spoiling fruits and vegetables, decaying leather, and many other materials belong to this genus.

Penicillium is one of the most prolific of the fungi. Each plant produces thousands of branching conidiophores bearing long chains of conidia. These become distributed so extensively that there is scarcely a square foot of surface in the vicinity of human habitations that is free from them. It is no wonder that they are so important in food spoilage.

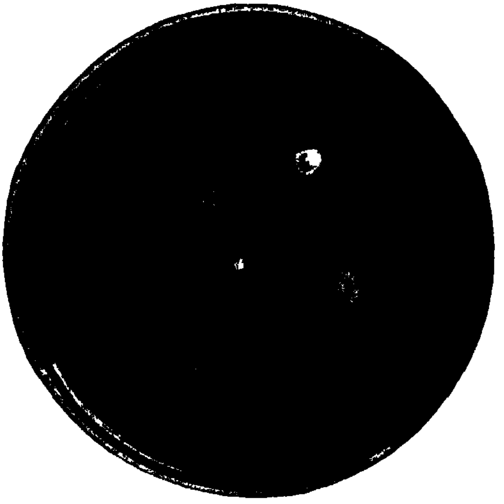


FIG. 197. *Penicillium.* Colonies growing in a culture dish.

Sexual reproduction, on the other hand, is rare, and in some species it is unknown. Conjugation and ascospore formation have been studied only in a general way, and the finer details have yet to be investigated.

Saccharomyces

It is probable that the *Saccharomyces,* or yeast plants, are Ascomycetes that have "degenerated" through the loss of their mycelium. In this evolutionary process it is supposed that fungi living in sugary solutions developed considerable variation in the production of mycelium and that those lines with little mycelium, since mycelium was not required for their mode of life, degenerated into yeast plants. For the most part yeasts are unicellular and round or elliptical in shape. They reproduce by budding and less commonly by ascospores, usually four to a cell. Conjugation between cells has been observed in some species as a preliminary to ascospore formation.

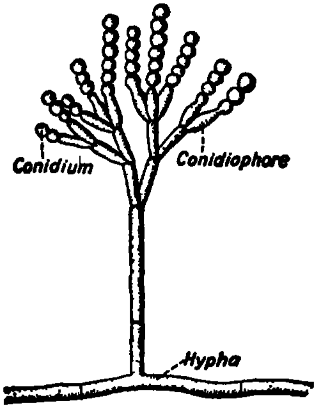


FIG. 198. *Penicillium.* Conidia produced on branched conidiophores.

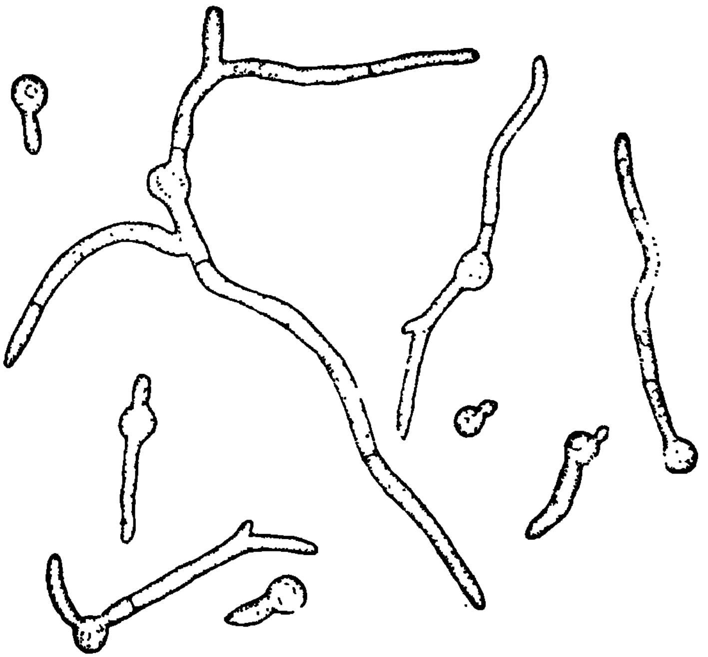


FIG. 199. *Penicillium.* Spores germinating and forming a mycelium.

Most species of yeast plants grow best in solutions rich in sugar. They have the power of breaking down the sugar into carbon dioxide

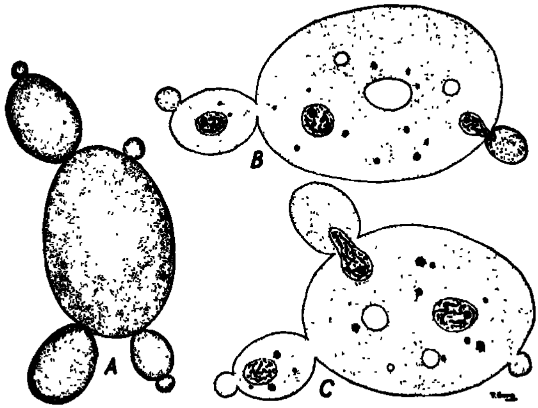


FIG. 200. *Saccharomyces* reproducing by budding. A, external view; B and C, sectional views to show nuclei. Somewhat diagrammatic.

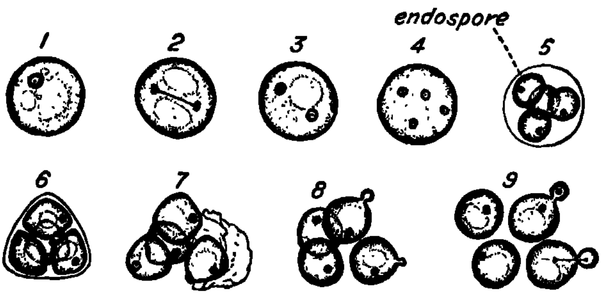


FIG. 201. *Saccharomyces*. 1 to 7, ascospore formation; 8, 9, budding. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Guillermond.)

and alcohol. In bread-making the carbon dioxide forms bubbles in the dough, causing it to rise. Both it and the alcohol are driven off during the process of baking. In the production of fermented liquors most of the carbon dioxide escapes into the air, leaving the alcohol behind.

Cup Fungi

One sometimes sees in rich moist woods, on the ground, on old logs, or on manure, the fruiting bodies of fungi that grow in the form of cups. Most of these are Ascomycetes that, because of their shape, are called "cup fungi," "peziza cups," etc. These cups, which are large ascocarps, vary greatly in different species as to size, shape, and color. The largest are several inches in diameter, the smallest almost microscopic. Some form deep cups, others shallow ones like flat discs. Some are very regular, others very much distorted. Some are borne on stalks, but more are not. The color is generally whitish when young, turning brown with age; but other shades such as pink and red are not uncommon.

In the development of these fungi, germinating ascospores form a mycelium in the substratum. This mycelium develops in great abundance at certain points, and in some species that have received careful cytological study there is here a formation and fusion of antheridia and oogonia. From the zygotes thus produced grow branches bearing numerous asci inside of cups that are formed from the surrounding mycelium. As a result each cup when mature contains many thousands of asci lining it like a layer of velvet.

Most of the cup fungi have little economic importance. They grow saprophytically and doubtless take some part in decay, but a few are parasitic. The destructive brown rot of stone fruits, for example, is caused by a member of this group of fungi.

Morels

Among the commonest of the edible fleshy fungi belonging to the Ascomycetes are the morels. They are from two to four inches high and can be recognized by their irregular, stalked, fruiting bodies. The stalks are nearly white or dull yellow in color—one species brown. At the top of each is a brown fruiting body, which has many large, irregular, dark-colored pits containing numerous asci. Morels are sometimes called mushrooms, but that name is preferably restricted to certain Basidiomycetes. Morels are of fine flavor, and none of them are poisonous.

Truffles

Truffles are spherical in shape, varying in color from nearly white to brownish black, an inch or two in diameter, and produce ascospores in

FIG. 202. Morels. (From Campbell's *General Elementary Botany*, Thomas Y. Crowell Company. Photograph by E. J. Kohl.)

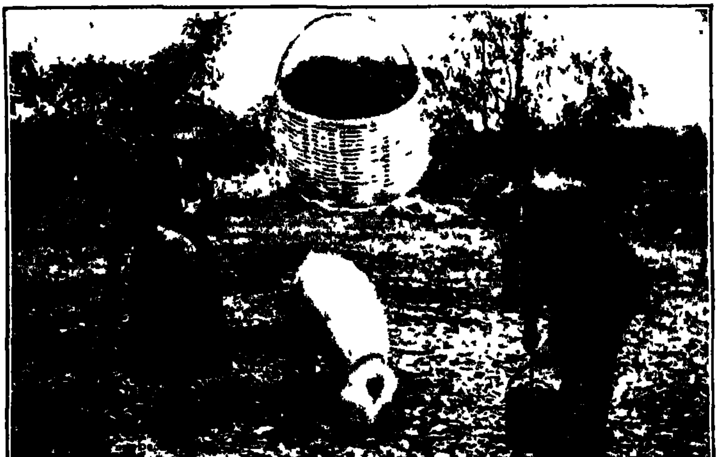


FIG. 203. Hunting truffles. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. Courtesy of Paita, Guérin et Jougla, Cahors, France.)

the interior. They are found chiefly in France and Germany, but a few occur in the United States. The best varieties are said to have the finest flavor of all the fleshy fungi, but they cannot be propagated artificially by any method now known, and as they grow underground most of them are never seen. They have a faint characteristic odor and some of the European peasants have trained pigs and dogs to find them. The animal is led about on a string, and when he scents a bed of truffles and starts digging he is given his reward in some other form while his master takes possession of the truffles.

Relationships of the Ascomycetes

The origin of the Ascomycetes is uncertain. They appear to have come from algae, either through the Zygomycetes or, more likely, directly from the Rhodophyceae or possibly the Chlorophyceae. There is some evidence in support of each of these three possibilities, but it is not complete enough to establish any one of them. The absence of a motile stage and the presence of a trichogyne on some Ascomycetes suggest their descent from Rhodophyceae. It is doubtful if the Ascomycetes gave origin to any other group of plants.

Basidiomycetes

The class Basidiomycetes is intermediate in size between the Phycomycetes and the Ascomycetes, there being something over 18,000 species. The most important groups are the rusts, the smuts, and the mushrooms.

Occurrence of the Basidiomycetes.—A large number of species are parasitic on the higher plants, causing diseases some of which are of great economic importance. Others, the mushrooms, puffballs, etc., are chiefly saprophytic, growing in manure and other organic matter. As a class they are very widely distributed on land, with no aquatic forms.

Vegetative Structure.—The Basidiomycetes are usually considered the most highly developed of the fungi. Few of them are simple filamentous saprophytes comparable in structure to *Rhizopus* and to *Penicillium*. Most of the Basidiomycetes are either highly specialized parasites or elaborately constructed fleshy fungi. The mycelium is regularly septate, and the cells are binucleate throughout a considerable portion of the life cycle. Colors of every description are occasionally found in fungi of this class.

FIG. 204. Some fleshy Basidiomycetes, showing variety of form. 1, bracket fungus, *Fomes ungulatus;* 2, sessile mushroom, *Crepidotus dorsalis;* 3, bird's nest fungus, *Cyathus striatus;* 4, earth star, *Geaster rufescens;* 5, coral fungus, *Clavaria cinerea;* 6, pore mushroom, *Boletus subtomentosus;* 7, stinkhorn, *Dictyophora duplicata;* 8, puffball, *Lycoperdon cyathiforme.* (1, 3, and 4 from Bresadola's *Iconographia Mycologica;* 2, 5, 6, 7, and 8 from Farlow's *Icones Farlowianae.*)

Reproduction.—As a rule no sharply distinguished asexual and sexual methods of reproduction are found among the Basidiomycetes. There is no motile stage, and there are no simple sporangia.

Definite *sex organs* are not produced by most species, but sexuality is well-nigh universal. Mycelial fusions are common, and the fusion of spores occurs in some groups and of nearly equal gametes in a few. By such means cells become binucleate, the two nuclei being unrelated, or at least not sister nuclei. They may be considered male and female, but they do not unite until a definite stage of the life cycle is reached, which may be weeks or months after the cells first become binucleate. As the mycelium grows, both nuclei divide, so that for a brief time there are two pairs in each elongating cell. Then the cell divides, each daughter cell receiving a pair of unrelated nuclei. This process continues until the time has come for the completion of the sexual process by union of the nuclear pair.

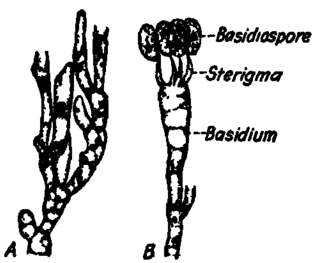


FIG. 205. Characteristic structures in Basidiomycetes. A, bit of mycelium of mushroom showing binucleate cells; B, basidium producing four basidiospores on sterigmata. (Redrawn from Harper.)

The most characteristic structure in the Basidiomycetes is the *basidium,* a club-shaped sporophore which bears four, or rarely two, *basidiospores* on tiny projections called *sterigmata.*

Ustilago avenae

Most of the smuts are rather strict, or obligate *parasites,* i.e., they are unable to pass through their life cycle without a living host. For the most part they attack meristematic regions—germinating seeds, floral parts, etc. *Ustilago avenae* attacks cultivated oats, causing the *loose smut* of oats.

The diseased grains of oats are black in color, masses of fungus spores having formed in place of the kernel. These spores are hardy enough to survive the winter. When germinating the next spring, they send out a germ tube which becomes the basidium and produces several basidiospores, the characteristic number in most fungi being four. They are one-celled, colorless, and capable of a brief saprophytic life

FIG 206 Smutted heads of oats

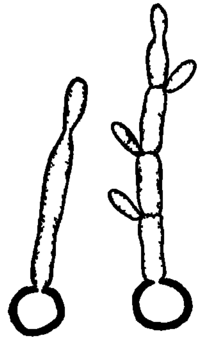


FIG 207 *Ustilago avenae* Spores germinating and forming basidia and basidiospores (From Duggar's *Fungous Diseases of Plants*, Ginn & Co)

FIG 208 *Ustilago avenae* Spores germinating on feathery stigma of oat flower (From George R Gage, Cornell Memoirs 109)

in which they reproduce by budding to form *sporidia* which resemble yeast plants.

Infection of the Host Plant.—It was formerly supposed that smut spores on the seed in the soil infected the sprouting grain and that infection took place at no other time and in no other place, but recent studies have revealed another and more complicated method. More commonly, infection takes place in the flowers. The germinating spores attack the feathery stigmas or the ovaries, and the mycelium becomes established in the coverings of the grains. Here it remains dormant until the following season when the seeds begin to germinate. The mycelium then becomes active and infects the developing embryo. Whether infection starts in the flower or in the young sprout, the host plant shows no symptoms of disease during its vegetative growth, but the fungus invades the growing-point of the stem and advances with it. When the plant heads out and the ovaries are formed, the parasite undergoes a period of rapid development and takes complete possession of them so that no embryo is formed. By a process of constriction the mycelium is divided into numerous spores which, as they mature, become thick-walled and black. The mycelium has binucleate cells, but the spores are uninucleate, nuclear fusion taking place just prior to their formation.

In certain other species of *Ustilago,* fusion takes place between two basidiospores or two conidia and thus the cells become binucleate, but *Ustilago avenae* has not been studied with sufficient thoroughness in this respect.

Some smut fungi have been found to be homothallic, while others are heterothallic, i.e., two different strains must be present to insure conjugation.

Seed Treatment.—This smut disease can be controlled by treating the seed grain with a suitable chemical, either formaldehyde or copper sulfate solution. This kills the germinating smut spores that might otherwise attack the germinating seed, and also the mycelium lying dormant in the seed coats and ovary wall. Some other smuts, for example corn smut, have a different life cycle, making the seed treatment ineffective.

Puccinia graminis

The rusts are of even greater importance than the smuts, and the stem rust of wheat, caused by *Puccinia graminis,* is one of the most destructive. The rusts are strict parasites and *Puccinia graminis,* like many others, requires two unrelated hosts for the production of all its spore forms. Two of these are produced on wheat, rye, and certain

grasses, and two others on common barberry, a thorny ornamental shrub introduced from Asia into Europe and thence into the United States.

FIG. 209. Lower surface of leaf from barberry plant, showing cluster cups (aecia) of *Puccinia graminis.* (From Buller's *Researches on Fungi,* Longmans, Green & Co.)

Spermogonial Stage.[1]—In the full life cycle of this fungus, *teliospores* (see below) are produced on wheat and related plants late in the summer. These survive the winter and in the spring give rise to basidia that, in turn, form basidiospores. The four basidiospores produced on each basidium are identical in appearance, but in their later behavior it is seen that two are of plus strain and two of minus strain, essentially male and female.

If these spores are blown onto the leaves of susceptible species of barberry bushes in late spring or early summer, they germinate and attack the leaves, producing within them a tiny mycelium that takes its nourishment from the host plant. In a few days the mycelium from each basidiospore forms within the tissues of the leaf a tiny pocket-like *spermogonium.*[2] As the spermogonia grow, most of them break through the upper

[1] There is a difference in the use of terms applied to the reproductive bodies and stages of the rusts. The corresponding terms are therefore given as follows: pycnial stage = spermogonial stage; pycnium = spermogonium; pycniospore = spermatium; aecial stage = aecidial stage; aecium = aecidium; aeciospore = aecidiospore; uredinial stage = uredo stage; uredinium = uredo sorus; urediniospore = uredospore; telial stage = teleuto stage; telium = teleuto sorus; teliospore = teleutospore; basidiospore = sporidium.

[2] The terms spermogonia and spermatia were used in early cytological studies of the rusts when the latter were suspected of being male gametes. When opinion shifted, and they were thought to be spores, perhaps no longer functional, the terms pycnia and pycniospores were adopted. Recent evidence that they have a sex function suggests that we should turn back to the earlier terms.

surface of the leaf, but a few of them appear on the lower surface. Within the spermogonia very minute one-celled oval *spermatia* are produced in considerable numbers. As the basidiospores were of plus and

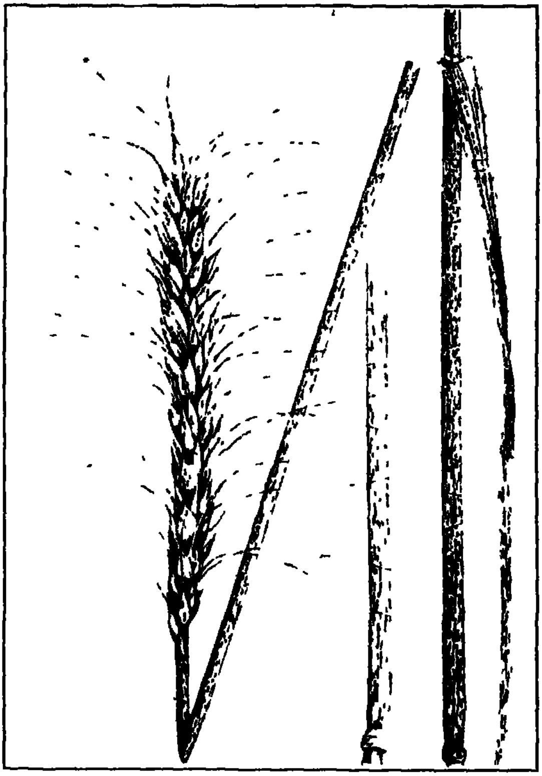


FIG 210. Wheat plants showing black stem rust caused by *Puccinia graminis*. (From Melchers & Parker, U.S.D.A. Bulletin 1046.)

minus strains, the spermogonia and spermatia developing from them are likewise plus and minus, i.e., of two sexes.

The sex differentiation now becomes evident. The contents of the mature spermogonia are exuded as sweetish, sticky droplets, which attract insects that carry the spermatia from one spermogonium to another. By this means plus and minus strains are brought together and a mycelium with binucleate cells originates. In this process a nucleus

from a plus spermatium or mycelial cell enters a cell of a minus mycelium or vice versa. The result is a mycelium each cell of which has two nuclei, one plus and the other minus. This mycelium develops into the aecial stage described below.

Aecial Stage.—This mycelium of binucleate cells now produces aecia, or "cluster cups," on the under side of the leaf, opposite the spermogonia. They produce spores in many chains packed tightly together. These aeciospores are nearly spherical, binucleate, and orange-red in

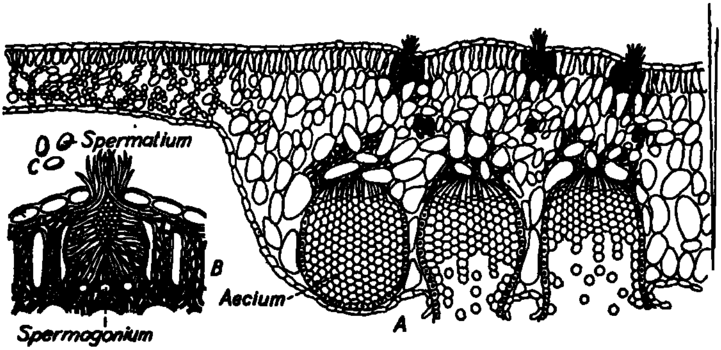


FIG. 211. A, section of barberry leaf infected with *Puccinia graminis* and producing spermogonia and aecia; B, section through spermogonium; C, three spermatia.

color. When the aecia rupture, the aeciospores are released and scattered by the wind. They are incapable of attacking the barberry but may attack wheat and to some extent other cereals and grasses.

Uredinial Stage.—The mycelium developed in the wheat plant from the attacking aeciospore, after a period of growth, breaks out through the epidermis of the stems and leaves in the form of orange-red pustules or *uredinia*. This is the "red-rust" stage. The *urediniospores* are one-celled and red in color, with roughened walls. They attack the same species of host as the aeciospores and rapidly spread the disease through wheat fields. The mycelium in the wheat plant continues to produce them as long as it receives an ample supply of carbohydrate food from the host.

Telial Stage.—Later in the season the mycelium inside the wheat plant starts producing teliospores instead of urediniospores. This change is brought about by a lowering of the sugar content of the host plant, either through a change in weather conditions or through maturity.

It is by this "black rust" stage that the greatest damage is done to wheat, but if the crop matures before the teliospore stage is reached the loss is relatively slight. The teliospores are two-celled, with a persistent stalk, or *sporophore*. Each cell has two nuclei when young, but these unite to form one before maturity. Teliospores have thick, dark walls and

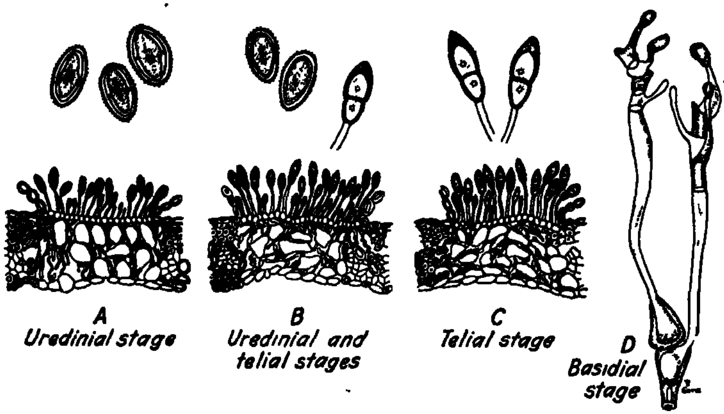


FIG. 212. *Puccinia graminis* in wheat leaves. A, uredinial stage; B, uredinial stage changing to telial stage; C, telial stage; D, basidiospore germinating and forming basidia and basidiospores. (D, after Tulasne.)

are hardy enough to survive a severe winter. They do not attack any host plant.

Basidiospore Stage.—In the spring following their formation the teliospores germinate. The nucleus in each cell is diploid. As the cell germinates and sends out a *promycelium,* or basidium, this nucleus divides, and its daughter nuclei divide again to form four. During these nuclear divisions the chromosome number is reduced to the haploid. From the basidium four tiny stalks, or *sterigmata,* are sent out. On the end of each a spore is formed by a process similar to budding. A nucleus enters each of these spores through the sterigma, leaving the old basidium without nuclei.

The basidiospores are one-celled, uninucleate, thin-walled, and nearly transparent. They can infect barberry but not wheat. Two of them are plus strain and two are minus strain.

Spore Forms of Puccinia graminis.—A tabular summary of the formation, character, and behavior of the five spore forms of *Puccinia graminis* is as follows on page 302.

Name	No. of cells	No. of nuclei	When formed	Borne on what host	Attacks what host	Longevity
Basidiospore	1	1	Early spring	None	Barberry	Very short
Pycniospore	1	1	Spring	Barberry	None	Very short
Aeciospore	1	2	Late spring	Barberry	Wheat	Very short
Urediniospore	1	2	Early summer	Wheat	Wheat	Short
Teliospore	2	1 per cell	Late summer	Wheat	None	Long

In Texas and other portions of the South, where the winters are short and mild and wheat of different dates of planting and also various grasses are growing practically throughout the year, the production of urediniospores is almost continuous. Under these conditions the disease can be perpetuated indefinitely by this spore form alone without the aid of the others.

Alternation of Generations.—The mycelium in the barberry leaf is at first uninucleate, but as it develops, and apparently through the influence of the spermatia, the number of nuclei increases to two or more. Each aeciospore that it produces has two nuclei which may be looked upon as two gamete nuclei that do not fuse at once. They attack the wheat plant and within its tissues form a binucleate mycelium which produces binucleate urediniospores and teliospores. As the teliospore germinates, the two nuclei of each cell unite, and this conjugate nucleus in the basidium then divides twice, forming four nuclei, one of which enters each of the four basidiospores. We see, then, that the gametophyte stage begins with the basidiospores and ends with the young aecial mycelium, while the sporophyte begins with the mycelium that forms the aeciospores and ends with the promycelium from the teliospores.

Life History.—*Puccinia graminis* is a rust fungus that requires two unrelated host plants to complete its life cycle. It attacks barberry leaves, forming in them a mycelium which is uninucleate. On the upper surface of the barberry leaves are produced spermogonia containing unicellular, uninucleate spermatia. On the lower surface are formed aecia containing unicellular binucleate aeciospores. These attack wheat, and the resulting mycelium has binucleate cells. It produces unicellular, binucleate urediniospores which also attack wheat. Later in the season the same mycelium produces two-celled teliospores in which nuclear fusion takes place. These live over winter and then germinate to form a promycelium, or basidium, in which the nucleus divides twice to form

four. The basidium then produces four unicellular, uninucleate basidiospores which again may attack the barberry.

Control of Stem Rust.—In warm climates, where wheat and different species of grasses provide a continuous series of susceptible hosts

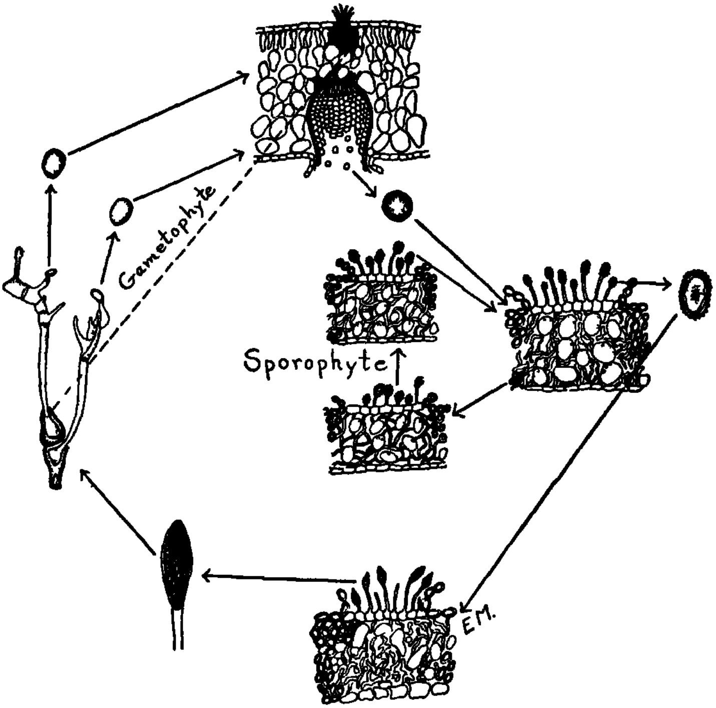


FIG. 213. *Puccinia graminis*, life history.

during nearly the entire year, urediniospores develop almost constantly and live long enough to bridge over any gaps in their production. Under these conditions no other spore forms are required to perpetuate the disease. In colder climates, however, such is not the case, and an effort has been under way in the states of the Middle West since about 1917 to control black stem rust of wheat by eradicating the barberry bushes, thus breaking the life cycle of the fungus. In the absence of the barberry the teliospores are produced just the same and develop basidiospores, but these die for want of a suitable host.

Barberry eradication throughout so large an area is a tremendous undertaking, for the bushes have been extensively planted, and in many places they have escaped from cultivation and are growing wild in large numbers.

The barberry eradication campaign appears to have brought about some reduction of this disease, especially in the eastern part of the eradication area, but the results are not all that had been hoped for. In 1927, 1935, and 1937 losses from wheat rust were heavy, but the average loss in the last decade has been much less than it had previously been. There is little doubt that a few urediniospores survive mild winters in the central United States and start spreading the disease the next season, and spores carried for long distances by the wind are an important source of infection. In late winter they may blow from the southern United States northward for many miles, finally settling on everything, including wheat fields. There they attack wheat and grasses, producing new crops of urediniospores which blow still farther north, and this process may be repeated until, by a series of steps, the extreme northern states and even Canada are reached. Generally infection brought about in this way comes later in the northern states than infection from barberries would have done had the bushes been allowed to remain, and is therefore less destructive.

Breeding for resistant varieties is also being carried on with considerable success, but a difficulty arises from the fact that *Puccinia graminis* has several biologic races differing from one another in their ability to attack different species and varieties of the host. Varieties of wheat resistant to the attack of one biologic race are liable to be susceptible to the attack of another. Apparently new biologic races originate by hybridization, i.e., a basidiospore from one biologic race forming a pycnium on a barberry leaf near another from a different biologic race may result in aeciospores of a new biologic race. Probably other biologic races die out in the "survival of the fittest." In some localities suitable hosts for certain races may be lacking. However, some varieties of wheat suffer less damage from the rust than do others. Especially is it true that winter wheats and varieties of spring wheat that mature early escape the most destructive infection. Some newly developed varities of spring wheat, notably Thatcher, have a high degree of resistance to the strains of *Puccinia graminis* found in certain regions. Kanred, a winter wheat developed in Kansas, resists well the strains that occur in the central United States but is susceptible to the attack of strains found in Minnesota and other northern states.

Heteroecious and Autoecious Rusts

Puccinia graminis, like many other rusts, requires two different species of host to complete its life cycle. Such rusts are called *heteroecious.* Other rusts complete their life cycle on a single host and are called *autoecious.*

Not every species of rust produces all five kinds of spores; indeed, any of these spore forms may be missing.

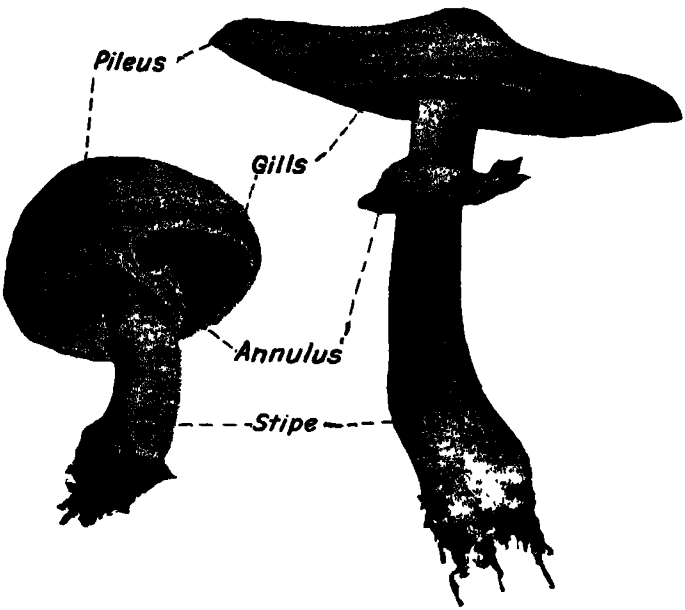


FIG. 214. Field mushroom, *Agaricus arvensis,* showing the different parts of the fruiting body. (Modified after Farlow.)

Mushrooms

The most conspicuous of the fungi are the mushrooms, which are commonly regarded as the most highly developed of the Basidiomycetes. They are all terrestrial and of wide distribution.

Vegetative Structure.—The mycelium arises from germinating basidiospores, either one or many. This penetrates the substratum where it is rather inconspicuous and becomes very abundant. The cells are, for the most part, binucleate.

Reproduction.—Under favorable conditions, often following a warm rain, the mycelium produces the characteristic fruiting bodies known as mushrooms or "toadstools."[1] A characteristic mushroom consists chiefly of a stout stalk or *stipe* bearing on its top a broad expanded portion, the *pileus* or cap, which suggests the top of an umbrella. In

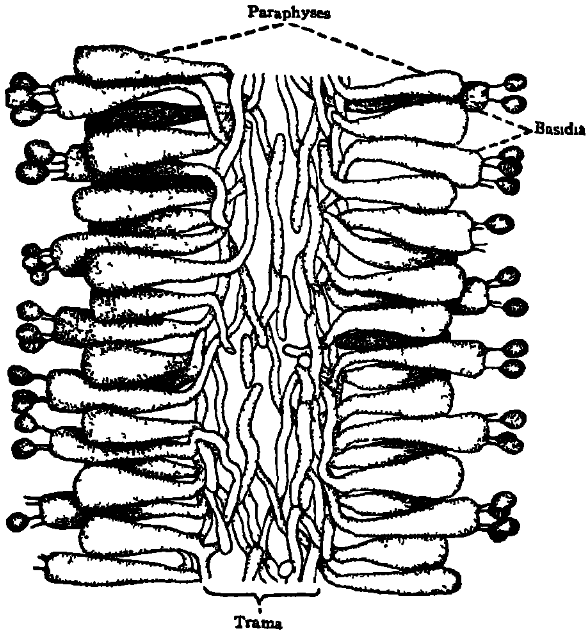


FIG. 215. Mushroom. Section through gill showing basidia and basidiospores (From Mottier's *Textbook of Botany*, P Blakiston's Son & Co)

a very young mushroom, a *velum*, or veil, extends from the stipe to the margin of the pileus. As the pileus elongates, this velum is broken away, leaving a ragged *annulus* about the stipe.

The spores are borne on the under side of the pileus, where gills are produced by most species. These gills are set vertically and radiate from the stipe, hanging suspended from the pileus. On the sides of the gills are produced innumerable basidia, each bearing, as a rule, four spores

[1] The edible species are often called mushrooms and the inedible species "toadstools," but better usage is to call all species mushrooms and to designate certain ones as edible and others as inedible or poisonous.

on sterigmata. The basidia of some mushrooms grow on the walls of pores instead of gills.

Sexuality of Mushrooms.—The spores are uninucleate, but the cells of the mycelium are binucleate, and the method by which they become so varies. A common method is by the union of mycelial branches from germinating spores. Some species are heterothallic and others are homothallic. The two nuclei of a cell show no tendency to unite during

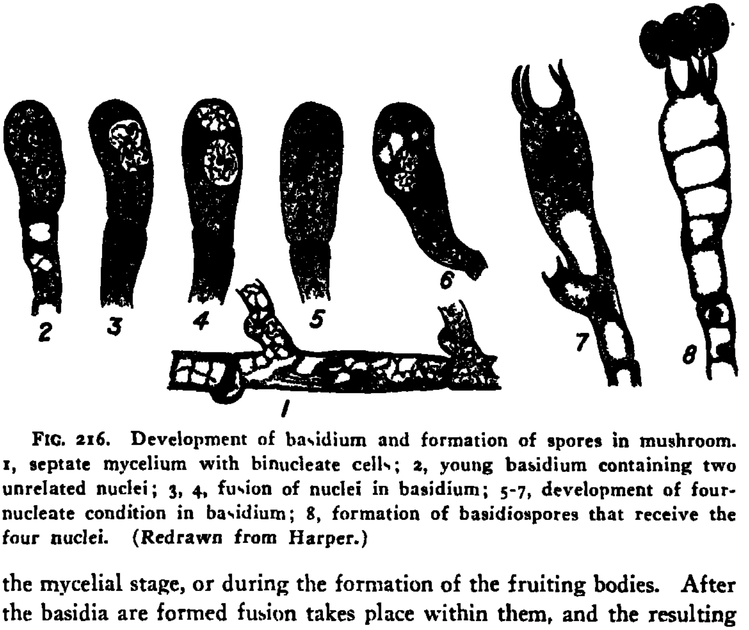


FIG. 216. Development of basidium and formation of spores in mushroom. 1, septate mycelium with binucleate cells; 2, young basidium containing two unrelated nuclei; 3, 4, fusion of nuclei in basidium; 5-7, development of four-nucleate condition in basidium; 8, formation of basidiospores that receive the four nuclei. (Redrawn from Harper.)

the mycelial stage, or during the formation of the fruiting bodies. After the basidia are formed fusion takes place within them, and the resulting nucleus divides twice, forming four. Each of these enters a basidiospore, and the old basidium is left with none. In the heterothallic species that have been studied closely, two of the basidiospores are plus strain and two are minus strain.

Edible and Poisonous Mushrooms.—Some species of mushrooms are edible; others, because of their texture or flavor, are unpalatable, and a few are poisonous. The only rule for distinguishing the edible from the inedible mushrooms is to know the species in question and its properties. Any other rule has too many exceptions to be reliable.

FIG. 217. *Agaricus campestris.* Lower three figures show the wild form; upper six figures the cultivated variety. (From Farlow's *Icones Farlowianae,* Harvard University.)

Agaricus campestris

One of the commonest members of this conspicuous group of fungi is the field mushroom, *Agaricus campestris.* It is widely distributed in nature, especially around manure heaps and in soil where manure has fallen. It is more common in open fields than in wooded regions.

Development.—From germinating spores a mycelium forms in the substratum, which develops slowly and after a few weeks produces dense masses just beneath the surface. These masses soon take the form of "buttons," which are the young, undeveloped, fruiting bodies less than an inch in diameter. These "buttons" and the accompanying mycelium are richly supplied with protoplasm and stored food. If favored by a warm rain they grow rapidly and expand into mature mushrooms. In this process the stipe elongates, the pileus broadens and produces gills which are attached to it but not to the stipe, and the velum is torn away, leaving a distinct annulus.

The mature fruiting body of this species is about two or three inches high. The pileus is about two and one-half inches across and relatively thick and firm. Its upper surface is more or less covered with flat, brownish scales. Its margin extends a little beyond the gills and is often fringed with remnants of the torn velum. The stipe is one-half to three-fourths of an inch in diameter and two to three inches high, with the annulus about half way up. In color the stipe is nearly white, the top of the pileus is light brown, and the gills change with age from a delicate pink to a dark brown.

As the spores ripen they are discharged from the basidia into the spaces between the gills and escape into the surrounding air. The number of basidia and spores is astounding. It has been calculated that one to two billions of spores are produced by a single mushroom of this species, and that they may be released at the rate of a half million to a million a minute. The spores continue to fall from the gills for two or three days but not at the maximum rate throughout the period.

Mushroom Culture.—While in foreign countries a number of different fleshy fungi are raised for food, in America *Agaricus campestris* is practically the only one. The industry has grown until nearly two million pounds are produced annually for market, nearly three-fourths of these in the vicinity of Philadelphia. The exacting requirements of mushrooms as to temperature and moisture are most easily met by growing them underground in caves, mines, or cellars, or under greenhouse benches.

Mushrooms do not grow readily from spores and hence mushroom culture involves two procedures. (1) A few companies with highly skilled workers produce "spawn," which is a mass of vigorous young mycelium growing in manure. Some of this is started from spores and some from tissue cultures of the young fruiting bodies. (2) By planting pieces of spawn in suitably prepared beds of manure the mushrooms of commerce are produced.

Comparatively few amateurs succeed in mushroom growing because of the exacting conditions and the skill required.

Puffballs

Puffballs differ from mushrooms in having a closed, more or less spherical fruiting body, which in most of the larger species is without a

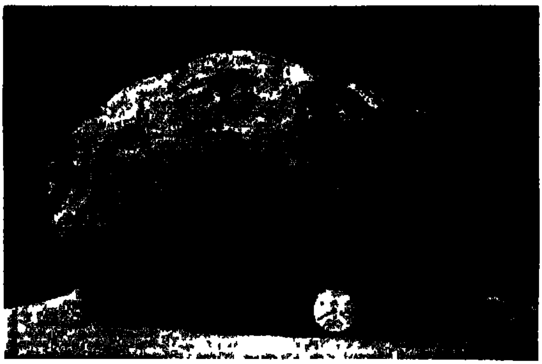


FIG. 218. Giant puffball, *Calvatia maxima.*

stipe. In size they vary from a fraction of an inch to a foot or more in diameter. The giant puffballs are the largest fungi known. The basidia with their basidiospores are borne internally. When ripe the spores form a black dusty mass inside. The puffballs are saprophytic and mostly edible, none of them being poisonous.

Relationships of the Basidiomycetes

The evolutionary origin of the basidiomycetes is unknown. Some accept the theory that they came from very low forms of life where the plant and animal kingdoms join. Others hold that they came from the Phycomycetes, and still others that they evolved from Rhodophyceae.

The rusts and smuts are generally considered more primitive than

the mushrooms and puffballs. Probably no other plants evolved from the Basidiomycetes.

Fungi Imperfecti

This term is applied either to fungi that have lost their *sexual* reproduction through degeneration, or to those in which it has been overlooked.

A few are doubtless Basidiomycetes, but the great majority are Ascomycetes that no longer produce ascospores but depend entirely on conidia and other kinds of asexual bodies for reproduction. The tendency to this form of degeneration among the Ascomycetes seems to be very pronounced. Some species of *Penicillium* produce ascospores so rarely that they seem almost to have become *Fungi Imperfecti.*

It has repeatedly happened that further study, using artificial cultures, has resulted in the finding of an ascospore stage in a fungus previously classed among the *Fungi Imperfecti.* This suggests that possibly none of these fungi have really degenerated, but that we have failed to find the sexual stage. However, some have been studied so exhaustively by a number of different workers that there remains little hope of finding such a stage, and it seems to have been permanently lost.

There are thousands of known species among the *Fungi Imperfecti,* many of them saprophytic and others parasitic. Some of the most important diseases of crop plants, including apple blotch, bean anthracnose, early blight of potato, and potato dry rot, are caused by them. The absence of a sexual stage has made the classification of this group into orders, families, and genera very difficult and unsatisfactory.

Economic Significance of the Fungi

A full statement of the economic significance of a group of plants involves a consideration of both their benefits and their harm to the human race.

Beneficial.—Certain fungi in each of the classes aid in the destruction of organic refuse and its incorporation into the soil. In this respect the Ascomycetes are more important than either of the other two classes. Yeasts are extensively used in bread-making and in the production of alcohol and alcoholic beverages. A small amount of food is obtained from mushrooms, puffballs, morels, and truffles.

Harmful.—Some sickness and death result from eating poisonous species of mushrooms. Many species of fungi are of major importance as causes of disease in economic plants, and a few cause disease in man and in domestic animals. Some species of Basidiomycetes cause decay of timber, both in standing trees and in lumber that has been cut. A vast amount of food spoilage is brought about by Zygomycetes, Ascomycetes, and *Fungi Imperfecti.*

Summary of the Characters of Fungi

The true fungi, using the term in the stricter sense, have certain characters in common: (1) predominating terrestrial habit, (2) lack of chlorophyll and consequent saprophytic or parasitic life, (3) filamentous structure, (4) terminal growth as distinguished from the intercalary growth common in algae, and (5) considerable differentiation into vegetative and reproductive portions.

Lack of chlorophyll in the fungi implies a dependence on organic material already formed by other kinds of life. Such a dependence necessitates enormous powers of reproduction, for only those spores that reach a favorable host or supply of organic matter can reproduce the fungus.

Comparison of Thallophyta That Have No Chlorophyll

Plants without chlorophyll are common among the thallophytes and are occasionally found even among flowering plants. Students of evolution agree that these plants do not all have the same immediate ancestors and are in doubt about the ancestry of some of them. There is considerable evidence that the bacteria and the blue-green algae are closely related, but whether the ancestral forms had no chlorophyll and acquired it to become the blue-green algae, or whether they had it and lost it to become the bacteria is a matter of controversy. Most authorities agree that each group listed in the table on page 313 had an ancestry different from that of the other groups, and the points of difference are here set forth for comparison.

TABLE SUMMARIZING THE THALLOPHYTA LACKING CHLOROPHYLL

Name of Group	Thallus	Asexual spores	Motile stage	Gametes	Approximate No. of described Species [2]
Schizomycetes	One cell	None [1]	Vegetative	None	1350
Myxomycetes	Plasmodium	In sporangia	Myxamoebae, zoospores, and gametes	Equal and motile	300
Zygomycetes	Non-septate mycelium	In sporangia	None	Equal and non-motile	500
Oomycetes	Non-septate mycelium	In sporangia	Zoospores, and occasionally gametes	Unequal and usually non-motile	800
Ascomycetes	Septate mycelium	As conidia	None	Nearly equal and non-motile	37,500
Basidiomycetes	Septate mycelium	As conidia	None	Variable and non-motile	20,000

[1] The spores produced by bacteria are not reproductive in function and are not comparable to the spores of the other groups.

[2] As a considerable number of new species are described each year it is presumable that the total number of existing species is considerably higher than that given in this column.

Review Questions

1. Give (1) a restricted and (2) a broader meaning for the word "fungi."
2. Does it have a place in the regular categories of plant classification, and if so what is its rank?
3. To what *division* do the fungi belong?
4. Name the three classes of true fungi.
5. Arrange them according to size, i.e., number of species.
6. In what ways do the fungi resemble the slime molds?
7. In what ways are the fungi different from the slime molds?
8. In what ways do the fungi resemble the bacteria?
9. In what ways are the fungi different from the bacteria?
10. What vegetative character distinguishes the Phycomycetes from the other two classes?
11. Name the two sub-classes of Phycomycetes.
12. Give the generic and specific names of an example of each of the two sub-classes of Phycomycetes.
13. What is the chief point of similarity between the two?
14. What are the chief differences between the two: (1) as to the morphology of the asexual spores? (2) as to the morphology of the gametes?
15. Define: (1) mycelium, (2) haustorium, (3) hypha, (4) coenocyte, (5) rhizoid, (6) conidium, (7) sporangiophore, (8) gametophore, (9) sporophore, (10) heterothallic, (11) septate, and (12) columella.
16. Give the usual habitat of: (1) *Rhizopus*, (2) *Saprolegnia*, (3) *Phytophthora*.
17. Write out the full life history of *Rhizopus*, indicating what portions are gametophyte and what sporophyte.
18. Write out the full life history of *Saprolegnia*.
19. Explain why *Phytophthora infestans* does not produce oospores.
20. In what condition does this fungus survive the winter?
21. Explain the method by which late blight of potatoes may be controlled.
22. By what method of cell division do the asexual spores form in Zygomycetes and Ascomycetes?
23. How are new plants formed from asexual spores?
24. Give the origin of the ascus in most Ascomycetes.
25. How does an ascus differ from an ordinary sporangium?
26. Describe the origin of the ascospores.
27. Write out the life history of *Sphaerotheca humuli*.
28. Give the usual habitat of: (1) *Sphaerotheca*, (2) *Penicillium*, (3) *Saccharomyces*, (4) morels, (5) truffles, (6) cup fungi.
29. How does the asexual reproduction of the Zygomycetes differ from that of the Ascomycetes?
30. What is an ascocarp? A perithecium?
31. What is supposed to be the function of the appendages of the perithecium?

32. In what condition does *Sphaerotheca* survive the winter?
33. Describe the structure of a yeast plant.
34. What is the evidence that it belongs to the Ascomycetes?
35. In what respect does it show degeneration as compared with other Ascomycetes?
36. Give two examples of edible Ascomycetes.
37. By what method of cell division does the mycelium become septate?
38. What is meant by *Fungi Imperfecti?*
39. What morphological character distinguishes the Basidiomycetes from other fungi?
40. Explain how basidiospores are formed on a basidium.
41. Name three important groups of Basidiomycetes.
42. Give the generic and specific names of an example of each of these groups.
43. Give the plural and singular forms of the following: (1) ascus, (2) sporangium, (3) basidium, (4) haustoria, (5) algae, (6) fungi, (7) conidia, (8) hyphae, (9) nucleus, (10) perithecia.
44. What is the color of most fungi?
45. Write out the full life history of *Ustilago avenae.*
46. Explain the method of controlling oat smut.
47. What are the usual host plants for *Puccinia graminis?*
48. Name other host plants commonly attacked.
49. Name all the kinds of spores formed by *Puccinia graminis.*
50. On what host plant is each formed?
51. What host plant can each attack?
52. Give the number of cells in each.
53. Give the number of nuclei per cell in each.
54. Explain how the eradication of barberry bushes in the northern United States may be expected to reduce the prevalence of wheat rust.
55. Explain why in the southern United States wheat rust would still be prevalent even though all barberries were removed.
56. What is the distinction between a heteroecious rust and an autoecious rust?
57. Describe the development of a typical mushroom, naming all parts in the sequence of their formation.
58. How does a puffball differ from a mushroom?
59. Why should not morels be classed as mushrooms?
60. What is the probable origin of the true fungi?
61. Give the economic significance of fungi: (1) beneficial, (2) harmful.
62. Compare algae with fungi, pointing out all similarities and differences

CHAPTER XXI

THALLOPHYTA—LICHENS

Among the peculiar and interesting Thallophytes the lichens merit more attention than they usually receive. They are often popularly

FIG. 219. Foliose lichen (*Parmelia sulcata*) on base of willow tree.

called "mosses," but the true mosses, discussed in the next chapter, are quite different and belong to a separate division of the plant kingdom.

Occurrence.—Lichens are seen the world over in the form of crusts on rocks, stumps, decaying logs, old board fences, and trees. They also grow on the ground, and those known as "reindeer moss" cover large areas and extend far into the north.

Vegetative Structure.—Lichens vary in size from a fraction of an inch to a foot or more in diameter. They commonly form broad scales or crusts but may dangle from the branches of trees in strands several inches long—some of them even a foot or more. They are usually grayish-green in color, but some species are dark green, yellow, red, brown, or almost black.

When studied with the microscope lichens are seen to be a combination of plants—an alga living with a fungus. The union between the two is very intimate, and in some cases neither can live without the other. Often the fungus sends haustoria into the cells of the alga. Lichens have a highly organized thallus with definite and characteristic form and an internal structure differentiated into layers, which in some species are analogous to those of a leaf, and with rhizoids for anchoring the plant to the substratum. In most lichens the fungus is much more prominent than the alga, making up more than half of its bulk and largely determining its form.

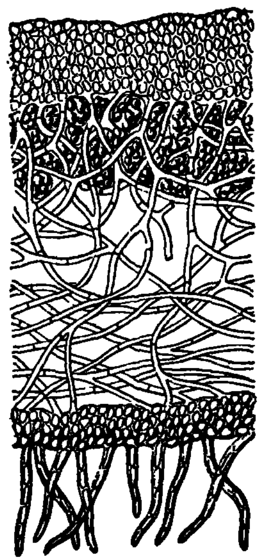


FIG. 220. Section of a portion of a lichen, *Strictina crocata*, showing specialized layers, the alga being near the top. (From Schneider's *Textbook of Lichenology*, Willard N. Clute & Co.)

Strictly speaking, the fungus and the alga in a lichen should be classified separately, each having its own generic and specific name. For purposes of convenience, however, a lichen is regarded as a single plant and is classified in the same way as are plants in general—family, genus, species, etc.—since its morphological characters are perpetuated throughout endless generations. It is, indeed, remarkable that two unrelated species could live in such intimacy and regularly form a highly specialized structure so closely simulating an individual plant.

Physiology.—Each plant making up a lichen plays its special part in the life of the whole. The fungus forms the main framework, the protective outer layer, and the rhizoids. Within its wefts is the alga, forming the major portion of one of the layers of the interior. The fungus, through its rhizoids in the substratum, supplies water and mineral mat-

ter, and doubtless it also takes some moisture from the air. The alga receives its share of these materials and carries on photosynthesis, thus supplying carbohydrates to itself and to the fungus. It should be realized that there is no intent to give; each plant makes its contribution involuntarily. The relationship between the fungus and the alga is a kind of symbiosis. Each symbiont apparently does more or less damage to the other, but the mutual benefit more than offsets the harm.

Reproduction.—The fungus in most lichens produces spores—generally ascospores. The alga usually does not. The spores of the fungus seem to play but a minor part in the reproduction of lichens and are as a rule wasted. In the first place, the likelihood that these spores, distributed by the wind, will come in contact with a suitable alga under conditions favorable to their joint development is not great. In the second place, it has been found by experiment that when they are artificially placed on algae of apparently the right species they usually are unable to make lichens.

Lichens have developed their own special method of propagation. Tiny bodies called *soredia* are formed. Each soredium consists of a bit of the alga wrapped in a weft of the fungus. These soredia are produced in great numbers and are distributed by wind and other agencies. Under favorable conditions they grow directly into new lichens, reproducing a practically perfect image of the parent. Sometimes, also, fragments of the old lichen, removed by accident, develop into new ones. Thus vegetative propagation has here become the principal method.

FIG. 221. Crustose lichen (*Rhizocarpon geographicum*) on red shale rock from Glacier National Park.

Relationships of the Lichens.—A very considerable number of fungus species are found in lichens but comparatively few species of algae. The fungus symbionts of most lichens are Ascomycetes; a few are Basidiomycetes. The algal symbionts generally belong to the unicellular Chlorophyceae or, less frequently, to the Cyanophyceae. Evidently fungi and algae of different kinds, at different times and places, derived benefit from associating in this way and thus developed a definite and permanent association. These strange forms have undergone con-

siderable evolutionary development since their origin, as shown by the remarkable differentiation in thallus and reproductive bodies found in the higher forms. The spores of the fungus symbiont appear to be only non-functional remnants from once independent ancestors in which they were doubtless of value.

Classification.—On the basis of their morphology three groups of lichens are commonly recognized. (1) *Crustose* lichens have little difference between upper and lower surfaces and but slight internal differentiation.

FIG. 222. Fruticose lichen (*Evernia vulpina*) on dead branch of pine tree.

They are small and compact and generally adhere firmly to rocks or other solid objects. (2) *Foliose* lichens are flat and leaf-like, although often much lobed. Upper and lower surfaces are distinctly different, and there is much internal differentiation. They vary greatly in size and commonly grow on the soil. (3) *Fruticose* lichens have cylindrical or flattened strands radiating from a center. These strands are usually much branched and may be either erect or pendent. They tend to grow on trees and dangle from the branches in pale green or grayish masses. The crustose forms are considered the most primitive and the fruticose the most highly developed.

Economic Significance.—Some lichens are palatable to livestock and are quite nutritious, but they are rarely abundant enough to be of much significance. The most important of these are the "reindeer moss" and the "Iceland moss" that supply feed for thousands of caribou and other animals in arctic regions.

Some chemicals are extracted from lichens, litmus being among the best known.

Review Questions

1. Does the word "lichen" have a definite place in the categories of plant classification and if so, what is its rank?
2. Is a lichen a plant? Explain.
3. Do lichens belong to a definite division of the plant kingdom? Explain.
4. In what habitat are lichens commonly found?
5. Name the three general groups of lichens and give the distinctions between them.
6. Describe the internal structure of a lichen.
7. What term is used to describe the relationship of fungus and alga in a lichen?
8. Explain how the symbiosis in lichens operates.
9. How do lichens reproduce?
10. Give the economic significance of lichens.

CHAPTER XXII

BRYOPHYTA—LIVERWORTS AND MOSSES

Among the first of the land plants, originating long after the algae had become established in the sea, were the liverworts and mosses. Even though they came into being so long ago they are still relatively simple. They constitute the Bryophyta, which is the next to the lowest division of the plant kingdom.

HEPATICAE—LIVERWORTS

Along streams in wooded regions, in open marsh lands, and sometimes on wet rocks, the close observer may find little flat green plants an inch or more in diameter, without true roots, stems, leaves, or flowers. People who are less observing often walk or sit on them without noting their presence, for they may be obscured by grass and other vegetation. These inconspicuous plants are liverworts, so called because of the lobed appearance of the thallus. Other kinds have the appearance of delicate vines a few inches long, with slender stalks to which are attached numerous tiny green leaves. Liverworts form the lower of the two classes of the division Bryophyta.

Marchantia polymorpha

Marchantia polymorpha is one of the commonest of the liverworts and is somewhat more specialized than most other members.

The thallus is one to three inches long, broad and flat, and dark green in color. It extends along the ground, leaf-like, with blunt lobes that result from dichotomous branching. Running lengthwise through the middle of the main plant and out into each branch is a depressed midrib ending in a notch at the end of each branch. The surface is laid off in tiny diamond-shaped or rhomboidal areas. On the under side an extensive system of hair-like rhizoids extends from the midrib down into the soil. Although not true roots they serve somewhat the same purpose, anchoring the plants and absorbing a little water.

A definite aeration system is found in *Marchantia,* though not in all

the liverworts. Just beneath the upper epidermis is an extensive series of air spaces, each corresponding to a rhomboidal surface area. Every one of these spaces communicates with the outside air through a stoma that is quite different from those of higher plants. It is bounded by about 16 cells fitted around the pore like a chimney. These stomata are constantly open. From the floors of the air spaces rise many short

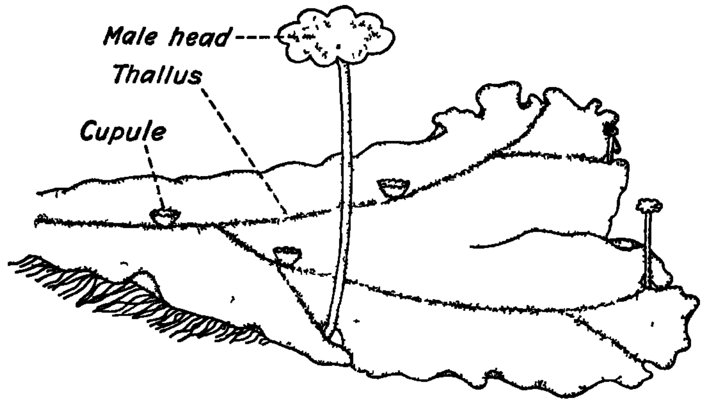


FIG. 223. *Marchantia.* Male plant composed of thallus, three male heads, and three cupules containing gemmae.

chains of cells filled with chloroplasts. These do most of the photosynthetic work.

Marchantia is heterothallic, or dioecious, the two kinds of gametes being produced on separate but morphologically similar thalli.

Reproduction.—*Marchantia* and some other liverworts have a well-developed means of vegetative propagation. At intervals on the midribs of both male and female thalli there form tiny *cupules*, each of which produces a cluster of *gemmae* in the bottom. Each gemma is a kind of bud that starts as a single cell which develops into a tiny thallus barely visible to the unaided eye. These gemmae, when distributed, grow directly into new plants.

Marchantia has more highly specialized structures for sexual reproduction than have other liverworts. From the marginal notches of male plants arise stalks that are in reality continuations of the branches of the thallus that bears them. Each stalk is surmounted by a *male head.* This head is disc-shaped, with a scalloped margin, and the antheridia that it bears are in little pits or depressions in the top surface. Each

antheridium contains numerous cubical cells which develop into antherozoids.* The antherozoids of these plants are elongated, blunt at one end and tapering toward the other They are motile by means of a pair of cilia attached at the side near the anterior end

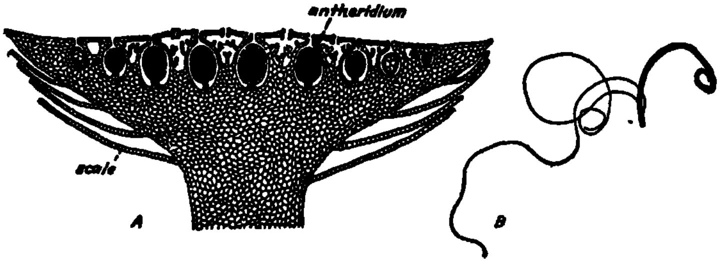


FIG 224 *Marchantia* A, vertical section through male head showing antheridial openings to the upper surface B, male gamete (From Smith, Overton et al, *Textbook of General Botany* The Macmillan Company)

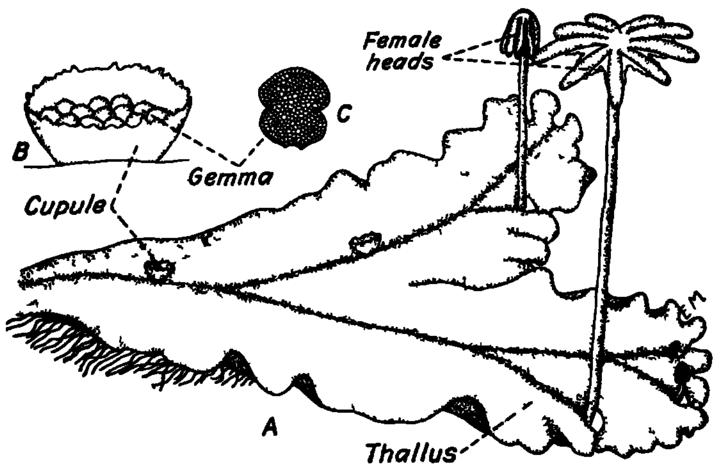


FIG 225 *Marchantia* A female plant with four female heads in different stages of development and with two cupules, B, cupule somewhat enlarged, C, gemma from cupule more enlarged

From similar notches in female plants slender stalks arise that bear *female heads* These heads are star-shaped with usually nine rays. Along the under side of each ray is a row of *archegonia* which open downward These *archegonia* are sex organs which are much more

highly developed than simple *oogonia.* In the Thallophyta the egg cell is protected by only a cell wall, but in the Bryophyta it is enclosed by a special layer of protective cells. The archegonium is flask-shaped and produces an egg in its base. Between the egg and the tip of the arche-

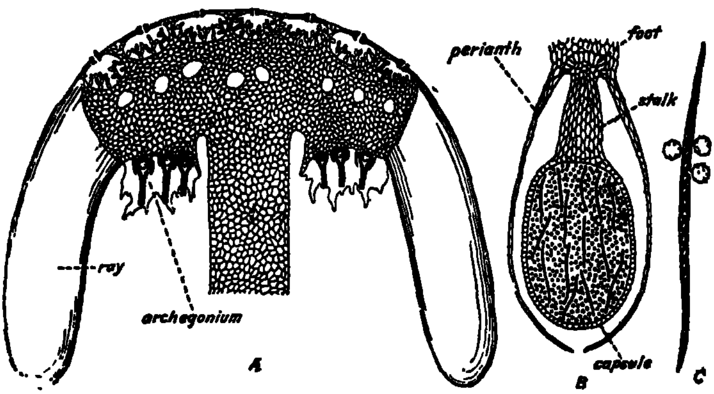


FIG. 226. *Marchantia* A, vertical section through a female head; B, sporophyte; C, an elater and three spores. (From Smith, Overton, et al., *Textbook of General Botany,* The Macmillan Company)

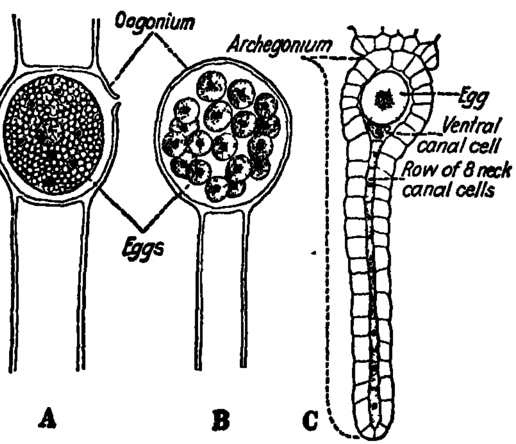


FIG. 227. Comparison of the structure of oogonia with that of an archegonium. (From Chamberlain's *Elements of Plant Science,* McGraw-Hill Book Company, Inc.)

gonium is a row of enclosed cells, usually eight. The basal one adjoining the egg is the *ventral canal* cell. The cells of this row disintegrate and thus make a canal or inlet for the antherozoids. These antherozoids are distributed by water or wind, and if they reach droplets of water around the tips of the archegonia they follow a chemical stimulus into and through the neck canals to the base, where one unites with each egg.

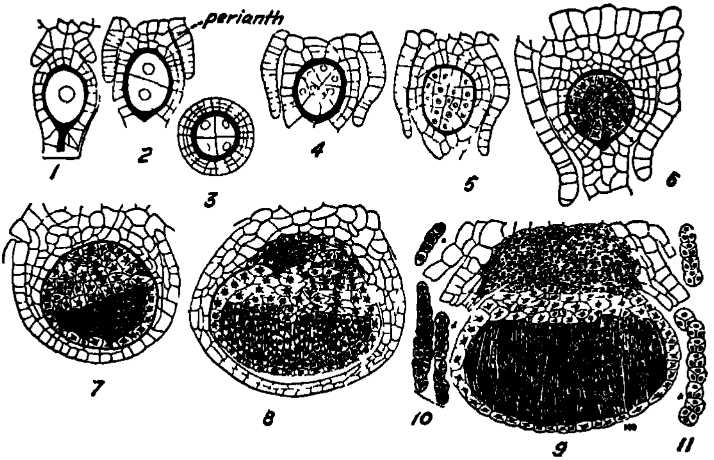


FIG. 228. *Marchantia.* Stages in the development of the sporophyte. 1, newly formed zygote in base of archegonium; 2-6, results of successive cell divisions of sporophyte; 7-9, differentiation of cells of sporophyte into tissues that will become the spores, the wall, and the stalk; 10, spore mother cells; 11, spores in groups of four. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. After Durand.)

The structures thus far described belong to the gametophyte generation. The fertilized egg, still inside the archegonium, by repeated cell division and growth now forms a sporophyte. This sporophyte, when mature, is very tiny and consists merely of a stalk, or *seta,* bearing a sac, the *capsule,* full of spores. In the process of spore formation a spore mother cell divides into four, two of which will produce male plants and two female plants. The sporophyte receives nourishment from the female head through its basal portion, the *foot,* and while young and green it carries on some photosynthesis. Among the spores are long, slender, spirally banded *elaters,* which, by coiling and uncoiling, help to eject the spores. Under favorable conditions each spore germinates to form a tiny alga-like plant that soon broadens out into a thallus.

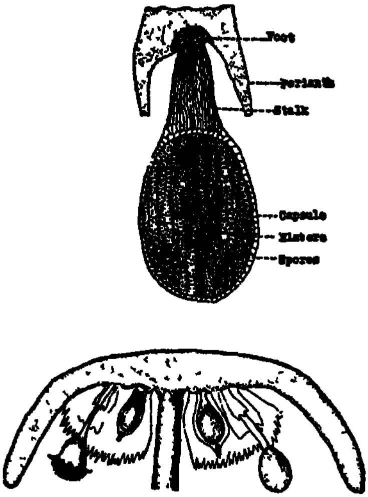


FIG. 229 Upper figure, young sporophyte with foot embedded in the female head (gametophyte) Lower figure, vertical section through female head showing four sporophytes in different stages of development (From Eyster's *College Botany*, Farrar & Rinehart)

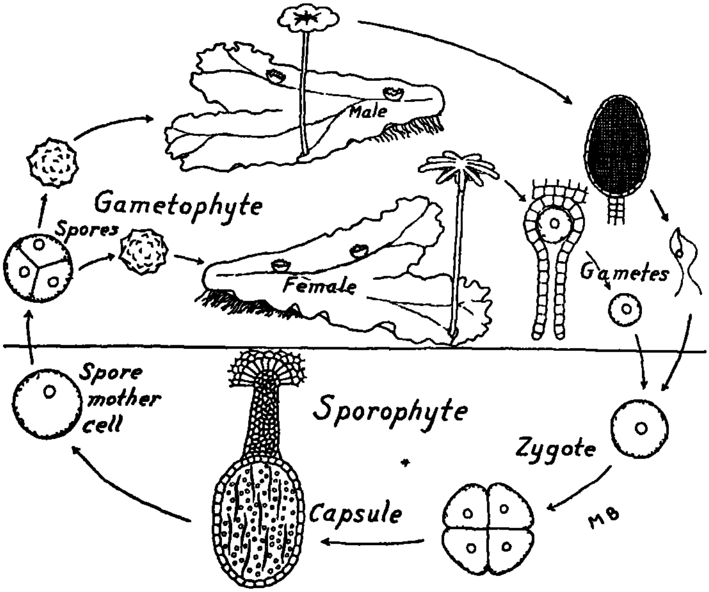


FIG. 230. *Marchantia.* Life history.

Alternation of Generations.—In *Marchantia* the gametophyte generation, with n chromosomes, includes the thallus, gemmae, male and female heads, antheridia and archegonia, and the gametes. The sporophyte, with 2n chromosomes, consists of the seta with its foot, the capsule, and the spore mother cells. As reduction in chromosomes takes place in the process of spore formation, the spores themselves have n chromosomes and consequently belong to the gametophyte generation.

FIG. 231. Moss plants, *Bryum*, growing on a rock. The leafy gametophytes have developed sporophytes from archegonia in their tips. These plants are similar in appearance to *Funaria*.

Life History.—*Marchantia polymorpha* is a small, green, flat thallus plant. It has vegetative propagation by means of gemmae. It is dioecious, male plants producing male heads bearing antheridia filled with antherozoids, while female plants produce female heads bearing archegonia, each of which contains an egg cell. Following fertilization the zygote develops into a sporophyte consisting of a seta, or stalk, bearing a capsule full of spores. These in turn produce new thalli, male and female.

MUSCI—MOSSES

Almost everyone who has access to the country is familiar with mosses—little leafy plants in dense masses or carpets. Unfortunately some other plants—lichens, and short, matted, small-leaved flowering plants—are also erroneously called mosses.

Funaria hygrometrica

One of the commonest of all the mosses is *Funaria*. Like most other genera of mosses it is commonly found in moist woods, on rocks, old logs, and banks of streams. The mature plants consist of green leafy stalks bearing at the top erect setae and capsules, which are green when young and yellowish brown when mature.

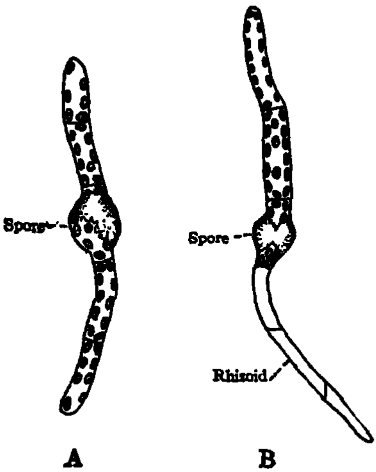


FIG. 232. *Funaria hygrometrica.* Spores germinating to form protonemata. (From Mottier's *Textbook of Botany,* P. Blakiston's Son & Co.)

Vegetative Structure.—To understand the structure of a moss plant its development must be followed. The green leafy plant is the gametophyte generation, and, as would be expected, it starts from a spore. This spore germinates and sends out a branching *protonema*—a little plant that looks much like a green alga. At intervals on this protonema buds are produced. These buds develop, growing into the leafy stalks and at the same time sending fibrous rhizoids down into the soil. The appearance of the plants in dense mats is explained in part by the close proximity to each other of germinating spores, the resulting crowded protonemata, and the number of buds developing on each; but extensive branching of protonemata and leafy stalks is often an important factor.

The leafy stalk has a central core of elongated cells that conduct some moisture, but it is not the morphological equivalent of the fibro-

vascular system of higher plants. Likewise the leaf-like structures on the moss are not homologous with those of ferns and flowering plants, for in the moss the leaves are part of the gametophyte while in the higher plants they are part of the sporophyte.

Reproduction.—When the leafy gametophyte plants of *Funaria* have reached their full size they produce gametes. These are in antheridia and archegonia standing erect on the tops of separate branches

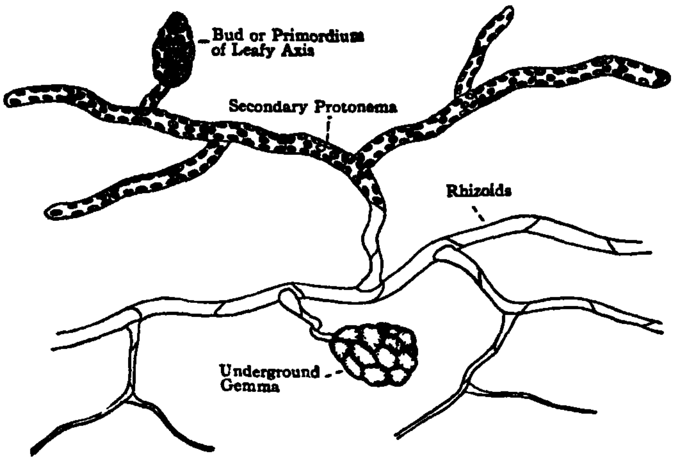


FIG. 233. *Funaria hygrometrica.* Protonema. (From Mottier's *Textbook of Botany,* P. Blakiston's Son & Co.)

of the same plant. In structure and function they are closely similar to those of *Marchantia.* Both are borne on the same gametophyte plant, although some mosses are dioecious and bear antheridia and archegonia on separate plants, and still others bear both of them on the tip of the same leafy stalk.

As in *Marchantia,* the antherozoids may be carried into drops of water that cover the archegonia and, passing through the neck canals, fertilize the egg cells. Although each female branch produces several archegonia and the egg cells of all may be fertilized, usually only one develops and the others wither away. This is a fairly common phenomenon in the reproductive bodies of higher plants.

The sporophyte formed from the zygote grows rapidly, and, bursting its way free, pushes up into the air, carrying the neck and part of the base of the archegonium up with it like a cap. This cap is called the

calyptra. The mature sporophyte consists of a slender seta an inch or so long with a capsule full of spores at the tip. It is at first bright

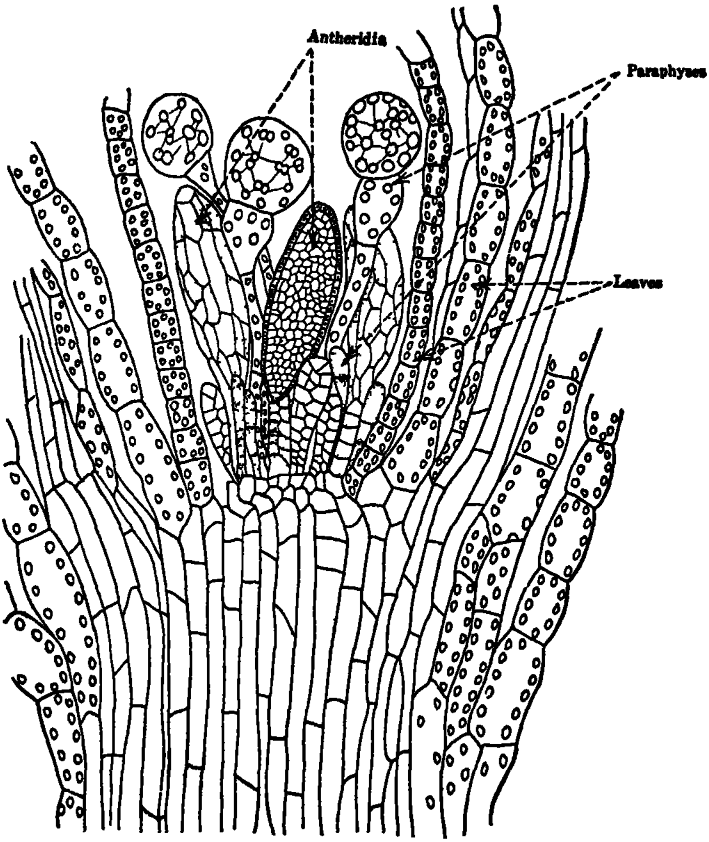


FIG. 234. Longitudinal section through the tip of a leafy axis of *Funaria hygrometrica,* showing antheridia. (Reprinted by permission from *Textbook of General Botany,* Third Edition, by Holman & Robbins, published by John Wiley & Sons, Inc.)

green but turns reddish with age. The spores are formed by two successive divisions of a spore mother cell. It is during this process of cell division that the chromosome number is reduced. The spore mother cell has the diploid number, but the spores have only the haploid num-

ber. The spores are liberated through a natural opening in the end of the capsule, which is covered by a lid, the *operculum,* until the spores are ripe. Around the opening is a border of teeth, the *peristome,*

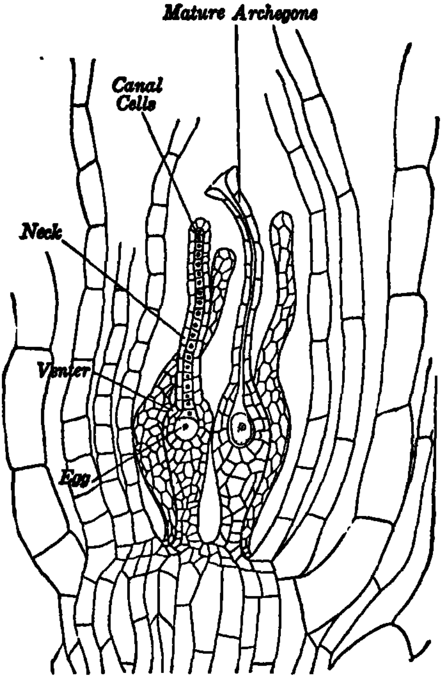


FIG. 235. Longitudinal section through the tip of a leafy axis of a moss plant showing archegonia. (From Smith, Overton, et al., *Textbook of General Botany,* The Macmillan Company.)

which bend in and out as a result of changes in humidity and thus aid in the liberation of the spores.

Life History.—*Funaria hygrometrica* is a small, green, leafy moss plant. The germinating spore forms an alga-like protonema which produces buds that grow up into leafy axes. Some buds of the protonema develop male branches bearing antheridia with antherozoids, and others develop female branches bearing archegonia, each containing an egg cell. Following fertilization the zygote produces a sporophyte consisting of a seta bearing a capsule full of spores.

Relationships of the Bryophyta

The division Bryophyta is composed of two sub-classes, the Hepaticae and the Musci. They appear to have evolved from the green algae, but there is a wide gap between all known green algae and the plants of this division. Similarity in archegonia, antheridia, and antherozoids indi-

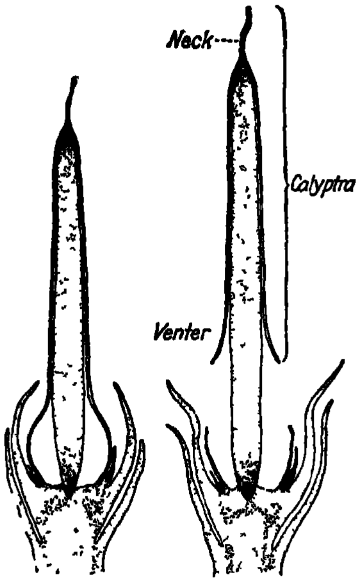


FIG. 236. A, tip of female moss plant showing development of sporophyte within the archegonium; B, same, but with the archegonium broken by the growth of the sporophyte, its upper portion forming the calyptra. (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company, Inc.)

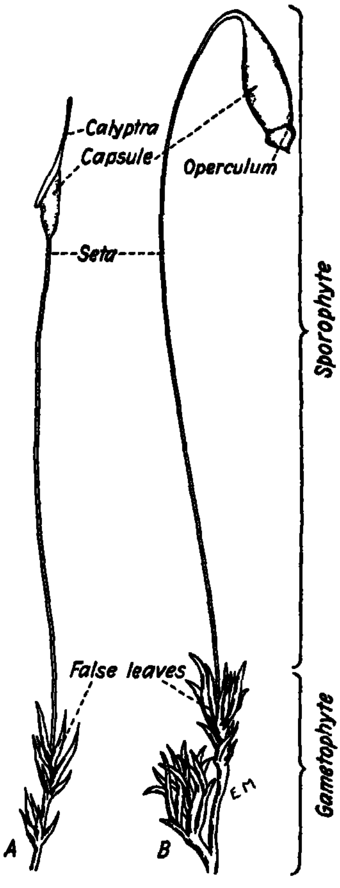


FIG. 237. Individual plants of *Bryum*. A, leafy axis bearing young sporophyte with calyptra on the top; B, leafy axis bearing nearly mature sporophyte.

cates a relationship between the liverworts, mosses, and ferns, but the character of the relationship is perplexing. It was long maintained that the liverworts were ancestral to the mosses and to the ferns, but evi-

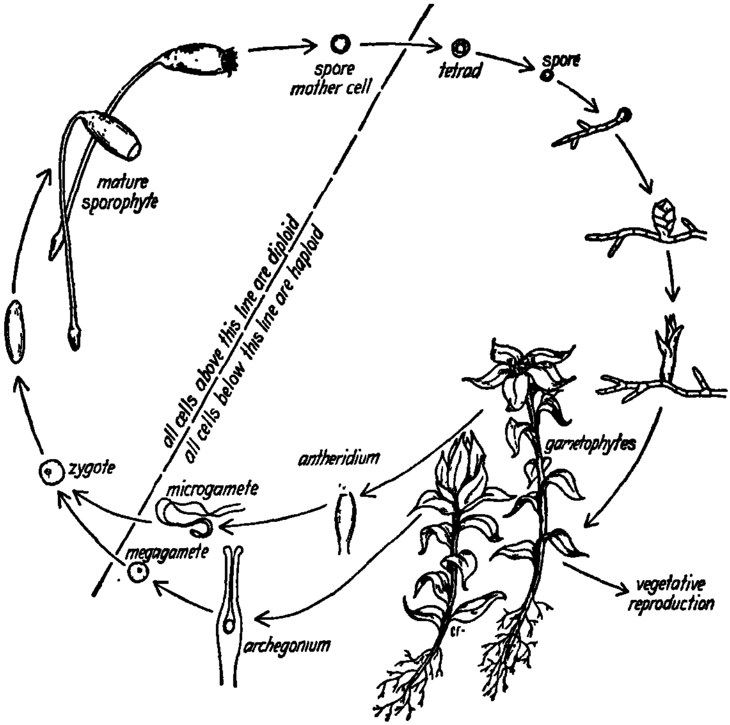


Fig. 238. ***Funaria.*** Life history. (From Robbins & Rickett's ***Botany,*** D. Van Nostrand Company, Inc.)

dence to the contrary has thrown doubt on this theory. In all likelihood no other groups of plants came from the mosses and perhaps none from the kinds of liverworts seen today.

Economic Significance

The liverworts are of practically no value to man except as interesting little plants that have been left far behind in the progress of evolution.

The mosses help to beautify the scenery along the banks of streams.

The peat moss, *Sphagnum*, has great power of absorbing and holding moisture and is somewhat resistant to decay even when wet. It is therefore extensively used in the packing of greenhouse plants for shipment. Much of the peat, which has considerable value for fuel, originated from *Sphagnum*. It is estimated that there is enough peat in the United States alone to make 12,000,000 tons of air-dried fuel.

Review Questions

1. To what division do the most primitive land plants belong?
2. What is supposed to have been their origin, i.e., their ancestors and the circumstances of their origin?
3. Which class of algae do the liverworts most resemble?
4. Give the common and the botanical names of the two classes of Bryophyta.
5. Describe the appearance of the thallus of *Marchantia*.
6. From what did it start?
7. Describe the appearance of the male heads.
8. Describe the appearance of the female heads.
9. Do the male and female heads and the thallus belong to the gametophyte or the sporophyte generation? Give reasons for your answer.
10. How does an archegonium differ from the oogonium of the Thallophytes?
11. Describe the antherozoid of *Marchantia*.
12. What is the origin of the sporophyte?
13. Describe its appearance in *Marchantia*.
14. Give the name and appearance of the structure that comes from the germinating spore of the moss.
15. What does it suggest with regard to the ancestry of the Bryophyta?
16. Why cannot the leaves of the moss be regarded as homologous with the leaves of higher plants?
17. How does the gametophyte of a moss obtain its food? The sporophyte?
18. Define: (1) archegonium, (2) gemma, (3) protonema, (4) calyptra, (5) antherozoid, (6) seta.
19. Write out the life history of *Funaria*.

CHAPTER XXIII

PTERIDOPHYTA—FERNS AND FERN ALLIES

The extensive use of ferns for decorative purposes has made these beautiful plants familiar to all. They are widely distributed in nature

FIG. 239. Tree ferns in a New Zealand forest. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc. Reproduced from *National Geographic Magazine*.)

and are extensively grown in greenhouses and residences. As we look at a fern what we commonly see is a cluster of great compound leaves, the stem at the surface of the ground being inconspicuous.

An Important Development.—Having just finished studying mosses, the student will need to readjust his outlook quite radically to comprehend the ferns. Whereas in the liverworts and mosses the gametophyte is the conspicuous portion and the sporophyte is small and simple, in the ferns the gametophyte is so small and short-lived that most people have never seen it, while the sporophyte has undergone a tremendous development resulting in the plants as we know them. After these facts have been fully appreciated the study of ferns will be easy; until then it may be difficult.

Ferns show considerable variation in morphological detail, but the following example is representative of one of the largest fern groups.

Polypodium

Different species of *Polypodium* are among the commonest of ferns. The plants have large, beautiful leaves, commonly spoken of as fronds, which are dark green in color and grow from an inconspicuous, partly hidden stem. Some of the leaves bear, on the under side, numerous tiny, brown masses of sporangia full of spores. This is the sporophyte generation.

The Gametophyte

As in the liverworts and mosses, the gametophyte develops from a germinating spore. The spores are one-celled but relatively large and thick walled. The germ tubes are similar to the protonema of the moss but shorter and stouter. As the tiny plant develops it becomes flat and green like the thallus of *Marchantia* but less than half an inch in diameter. It is called a *prothallium*. This pretty little prothallium is heart shaped, one layer of cells in thickness except near the center, and anchored to the ground by rhizoids. If we turn it over and examine it with a hand lens, we find that it bears two kinds of sex organs. It is therefore a gametophyte.

Antheridia.—The rhizoids grow mostly from the older, basal portion of the prothallium, and among them are found a number of short, broad antheridia, usually a half dozen to a dozen. Each of these produces, typically, thirty-two antherozoids.

Antherozoids.—The antherozoids of ferns are quite remarkable. Each consists of a long, coiled cell composed mostly of nuclear material with very little cytoplasm. It has a delicate longitudinal band, and from this extend numerous long cilia. When first discharged these antherozoids are very active, swimming through water with a spinning

motion. Evidence has been found that the archegonia of some ferns secrete a little malic acid. Experimentally, if one has a few fern antherozoids in a drop of water and introduces a little weak malic acid into the side of the drop they will swim vigorously toward it as it diffuses to them. It is fair to conclude, then, that in nature malic acid

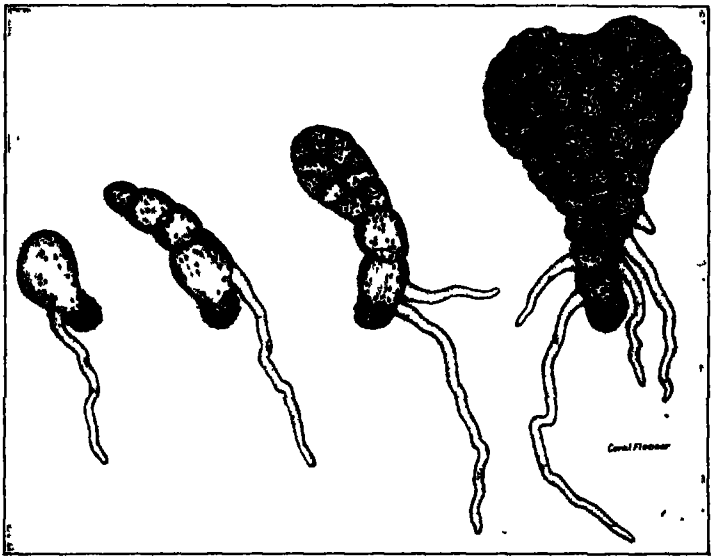


FIG. 240. Fern spores germinating to form a prothallium. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

is the substance that attracts the antherozoids into the archegonia and so to the egg cells.

Archegonia.—The archegonia are, in general, like those of the Bryophyta except that they are shorter and usually curved and are partly embedded in the prothallium. There is a similar layer of protective cells which encloses three cells in a row—an egg cell in the base of the archegonium, a ventral canal cell, and a single, binucleate, neck canal cell. The last two disintegrate, absorb moisture and swell, and burst open the tip of the archegonium, thus forming a continuous passage to the egg.

Fertilization.—The details of fertilization in *Polypodium* are not easily demonstrated, but if the known facts are pieced together the fol-

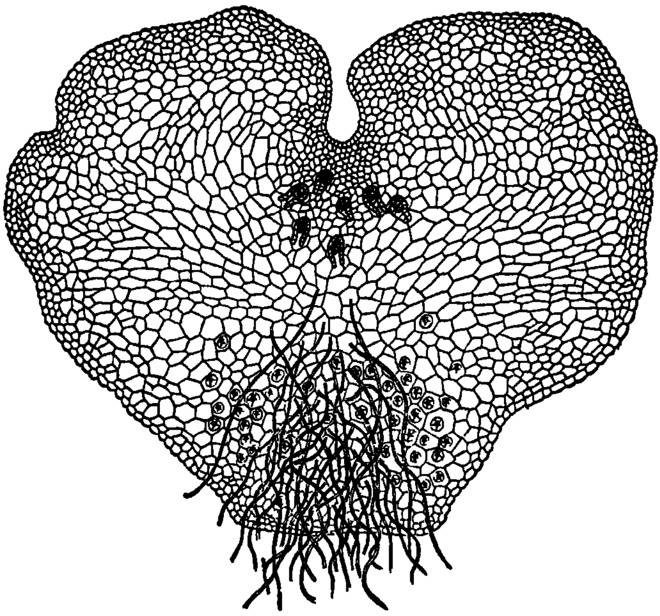


FIG 241 Fern prothallium View of the under side showing archegonia near the apical notch and antheridia among the rhizoids near the base (From Sinnott s *Botany, Principles and Problems*, McGraw Hill Book Company, Inc)

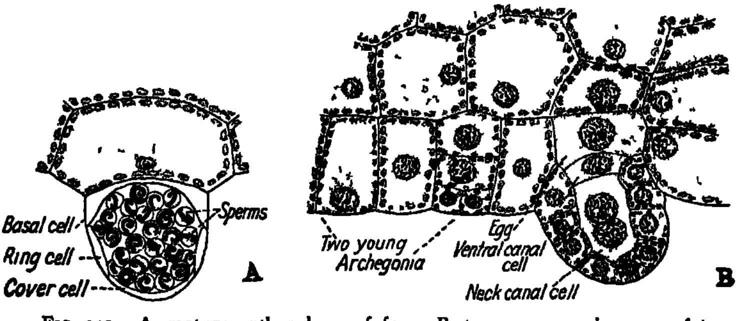


FIG 242 A, mature antheridium of fern, B, two young archegonia of fern and one mature one (From Chamberlain s *Elements of Plant Science*, McGraw-Hill Book Company, Inc)

lowing account is obtained. A single drop of water on the under side of the prothallium may be sufficient to include both the antheridia and the archegonia. *The antheridia open and discharge their antherozoids* into the drop of water. Directed by a chemical stimulus they enter the opening in the tip of the archegonium and pass through the canal

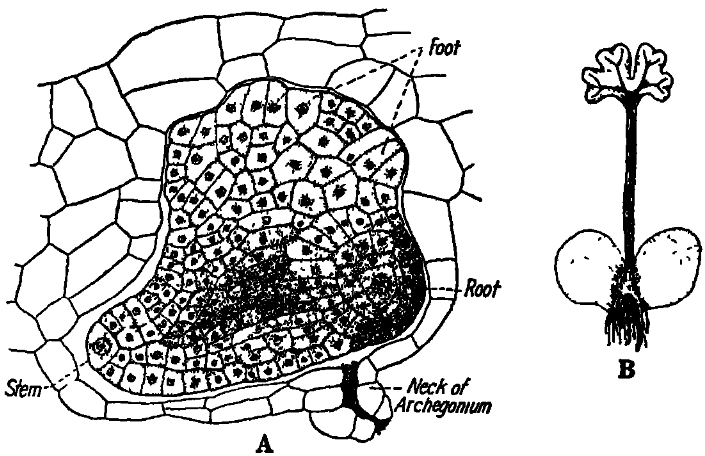


FIG. 243. A, young sporophyte of fern developing within the archegonium of the prothallium; B, sporeling of fern—a young sporophyte growing from the prothallium (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company, Inc.)

to the egg cell. Two or more archegonia may have their egg cells fertilized, but as a rule, only one of them develops.

The Sporophyte

Immediately after fertilization the zygote develops into a sporophyte. This sporophyte of the fern shows such a remarkable advancement over that of the moss that it must be given careful study. In the moss it consists of a single stalk an inch or two long, bearing a capsule of spores. There are no leaves or roots and it remains on top of the gametophyte from which it obtains nourishment, never penetrating the soil. In the fern, however, the young sporophyte sends a root into the soil and produces stems and leaves—the fern plant as we know it.

In its development, the zygote is nourished by the prothallium that produced it until it has formed a tiny root and a short stem bearing a

single leaf. Thereafter it leads an independent life and grows into the beautiful fern plant, while the prothallium withers away.

The Fibrovascular System.—Most of the common ferns have a half-buried stem a few inches long and leaves one to two feet high. Ages ago, however, there were tree ferns, fossils of which still remain, and

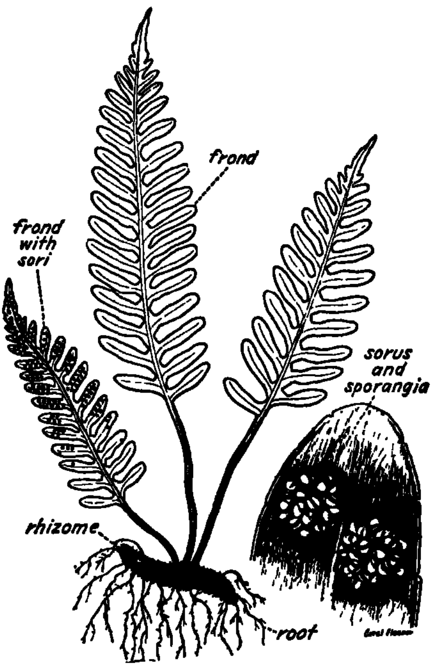


FIG. 244. *Polypodium vulgare.* (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

even now in the tropics a few ferns can be found that resemble palm trees, with their unbranched trunk a foot in diameter surmounted by a great tuft of leaves as much as fifty feet from the ground. Obviously a well-developed fibrovascular system is necessary to keep them erect and transport water to the top.

In *Polypodium* the fibrovascular bundles are variable in number but rather distinct from each other and separated by parenchyma. There is no cambium layer. Each bundle consists of a strand of xylem ensheathed by a layer of phloem. Outside the phloem is a pericycle, sur-

rounded in turn by an endodermis. The burden of supporting the weight of stem and leaves is shared by heavy strands of mechanical

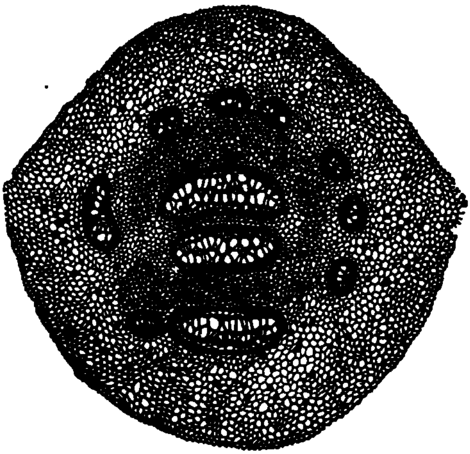


FIG. 245. Cross-section of fern rhizome, showing the distribution of fibrovascular bundles. (From Jeffrey's *Anatomy of Woody Plants*, University of Chicago Press.)

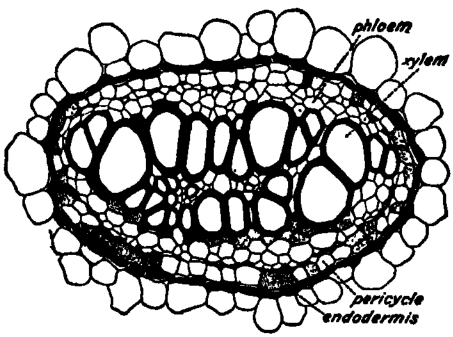


FIG. 246. Cross-section of a single fibrovascular bundle of a fern, with phloem surrounding the xylem. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

tissue outside the bundles and distinct from them. As in the flowering plants the bundles extend continuously from root to leaves.

Spore Formation.—Spores are produced on the under sides of the leaves. In general, spore-bearing leaves are termed *sporophylls*. In

some plants they are highly specialized and quite different from ordinary leaves, and even in some ferns spore production is limited to certain fronds, but in *Polypodium* there is no distinction between spore-bearing leaves and other leaves. On the under sides may be found conspicuous, small, brown bodies, the *sori*. Each sorus consists of a cluster of sporangia. The sporangia are borne on slender stalks, and each consists of a layer of cells enclosing a collection of spores. The number in each

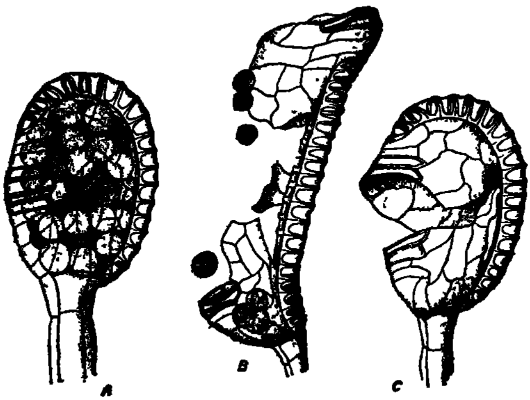


FIG. 247. Fern sporangia. A, unopened; B, discharging spores; C, empty. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

sporangium varies with the species, but in some it is typically sixty-four. They originate by two successive divisions of spore mother cells. During this process the chromosome number is reduced from diploid to haploid.

In a semicircle forming a part of the sporangium wall is an *annulus* consisting of a row of cells that are thin-walled on the outside and thick-walled toward the spore cavity. As the sporangium dries, the annulus shrinks unevenly and finally straightens out, breaking the sporangium open and partly shutting it again with a snap, thus flipping out the spores. These spores develop into a new crop of prothallia.

Life History of a Fern.—The conspicuous part of a fern is the sporophyte, which is large and green and composed of true roots, stems, and leaves. It reproduces by spores. These spores germinate to form prothallia—small, green, heart-shaped thalli that bear rhizoids, antheridia, and archegonia. The prothallia, sex organs, and gametes make up the gametophyte generation and have n chromosomes. Following

fertilization the zygote grows into a sporophyte with roots, stems, and leaves. This sporophyte has 2n chromosomes and bears on the under sides of the leaves spore mother cells that also have 2n chromosomes. By two successive divisions they each produce four spores with n chromosomes.

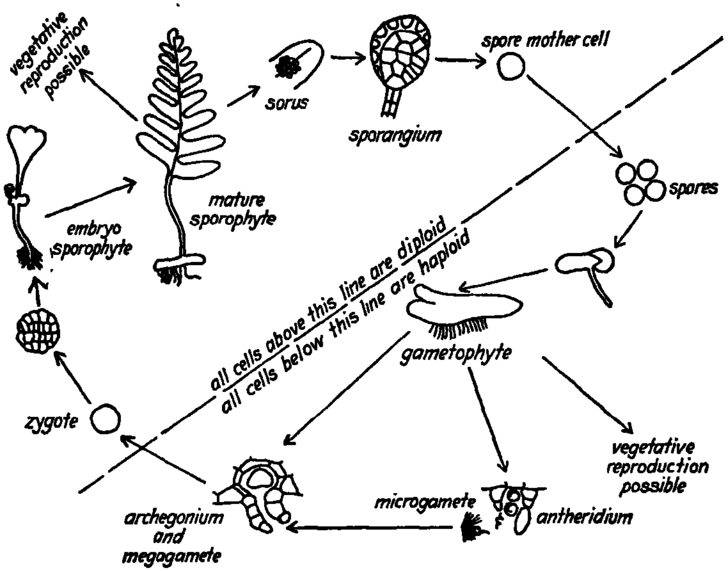


FIG. 248. Fern, life history. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

Two successive nuclear divisions in which the chromosome number changes from 2n to n are called reduction divisions, and the process of reduction is called *meiosis*.

SELAGINELLA

In the eastern, southern, and extreme western forests of the United States where the precipitation is abundant, there grow little, prostrate, evergreen plants with tiny leaves and a moss-like appearance. They are extensively used for decorative purposes, especially Christmas wreaths. They are called club-mosses, although not really mosses at all and very different from them in structure and life history. The

lesser club-mosses, which belong to the genus *Selaginella,* are grown in greenhouses and are more erect in habit but otherwise similar in appearance.

The Sporophyte

The graceful *Selaginella* plant is a sporophyte with green, scale-like leaves growing from a slender stem. The sporangia are borne in

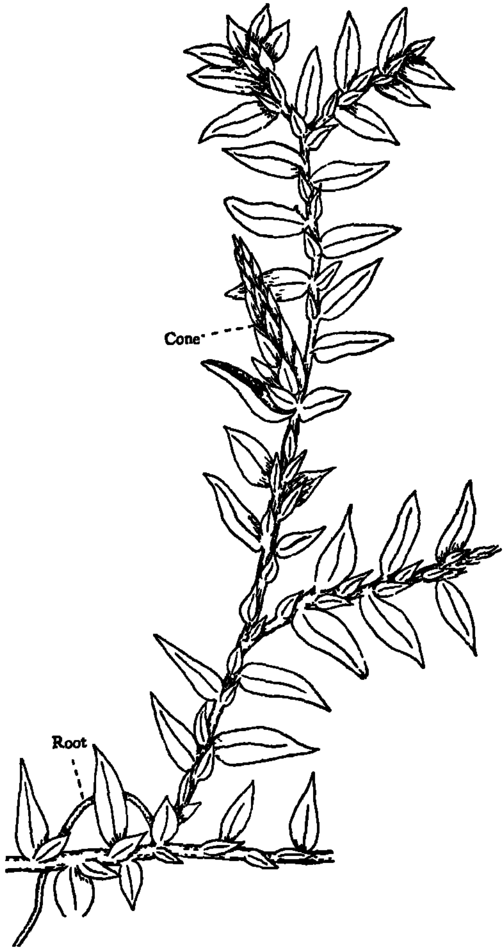


FIG. 249. Branch of *Selaginella* plant. (From Mottier's *Textbook of Botany,* P. Blakiston's Son & Co.)

definite *cones, or strobili,* at the tips of the stems, and now comes the significant difference between this plant and most ferns, for here are

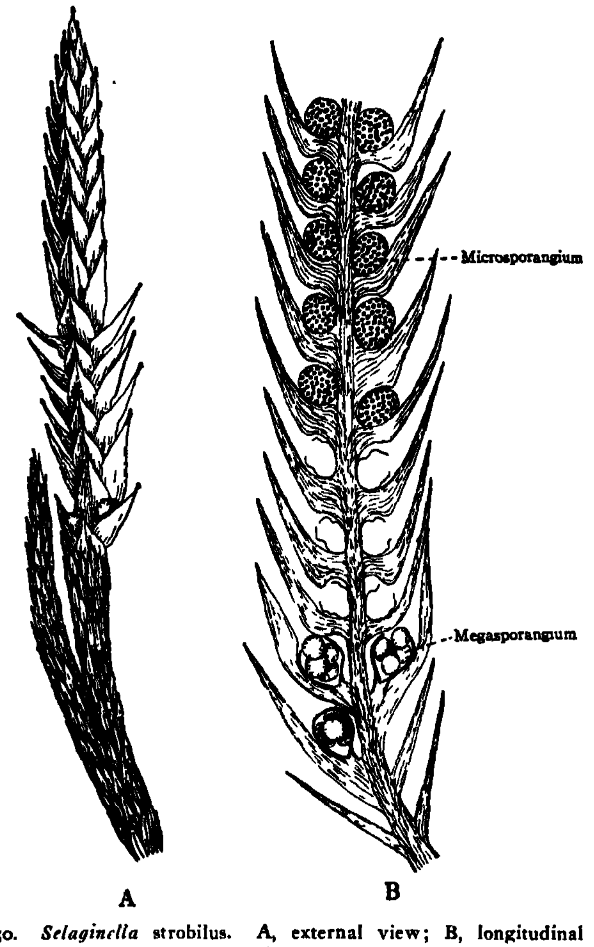


FIG. 250. *Selaginella* strobilus. A, external view; B, longitudinal section. (From Mottier's *Textbook of Botany,* P. Blakiston's Son & Co.)

found two kinds of spores. Each sporophyll at the base of the strobilus bears a sporangium with four relatively large *megaspores,* while each sporophyll higher up in the strobilus bears a sporangium filled with tiny *microspores.* This condition, in which two or more kinds of spores

are produced by the same plant, is called *heterospory;* while that found in *Polypodium,* where only one kind of spore is produced, is *homospory.* It is important to know that a few ferns have developed heterospory, and that it prevails in all the seed plants.

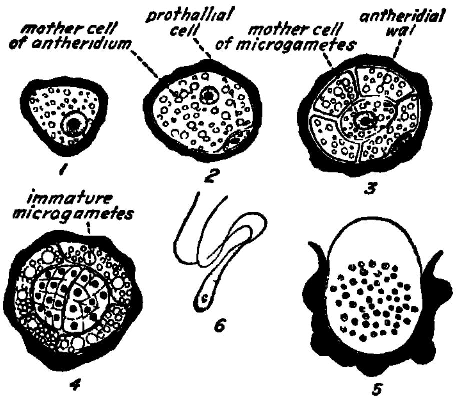


FIG. 251. *Selaginella.* Development of microgametophyte from microspore. 1, microspore; 2, 3, formation of prothallial cell, antheridial wall, and mother cell of male gametes; 4, 5, formation of male gametes; 6, male gamete. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc. After Lyon.)

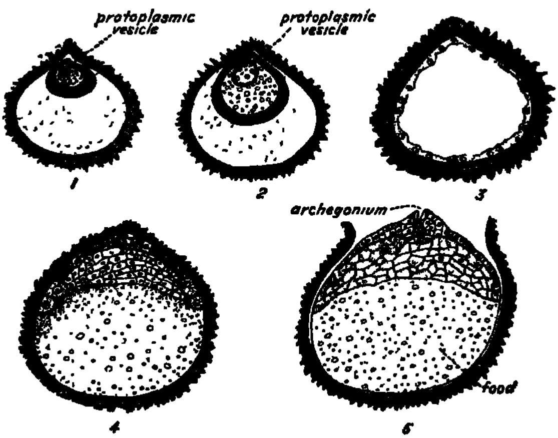


FIG. 252. *Selaginella.* Development of megagametophyte. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc. After Lyon.)

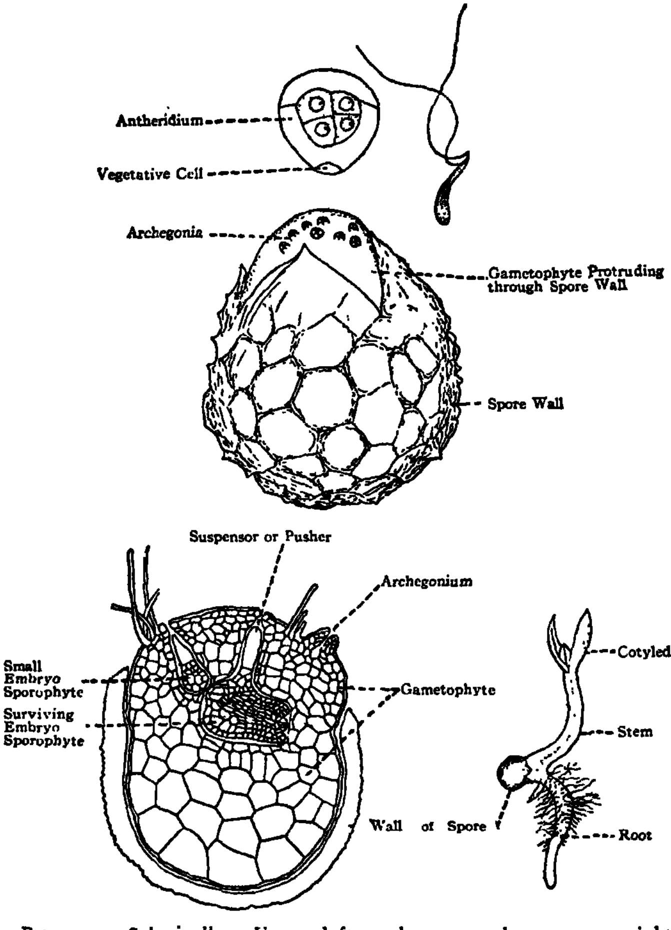


FIG. 253. *Selaginella.* Upper left, male gametophyte; upper right, antherozoid; center, female gametophyte partly within megaspore wall; lower left, sectional view of female gametophyte; lower right, young sporophyte growing from female gametophyte. (From Mottier's *Textbook of Botany,* P. Blakiston's Son & Co.)

The Gametophyte

The next steps in the life history of *Selaginella* must be closely followed. Spores germinate and make gametophytes. If there are two kinds of spores there must be two kinds of gametophytes.

The Male Gametophyte.—The development of a male gametophyte from a microspore is very simple. This one-celled spore enlarges a little but remains microscopic in size and by cell division forms an antheridium with a single vegetative cell at the base—nothing else. In the decline of the gametophyte nothing remains of the thallus but the one vegetative cell. The antheridium produces antherozoids somewhat like those of the Bryophytes.

The Female Gametophyte.—The megaspore swells somewhat and divides into a few dozens of cells which burst the spore wall but never wholly escape from it. This makes a round thallus barely visible to the unaided eye. It produces a few rhizoids and a few archegonia. This is the female gametophyte.

Development of the New Sporophyte.—If antherozoids are carried into a drop of water covering the female gametophyte, they enter the archegonia and fertilize the egg cells. One of these, or rarely two, develops, sending a root down into the soil and a leafy stem into the air. The tiny female gametophyte then withers away, and the sporophyte grows into a slender, branching plant several inches long.

Life History

Selaginella is a green, leafy plant, the conspicuous portion of which is the sporophyte. This bears strobili, the basal sporophylls of which produce megasporangia with four megaspores each, while the upper sporophylls produce microsporangia with many microspores. The microspores develop into microscopic male gametophytes with one antheridium each, while the megaspores develop into tiny female gametophytes, each bearing a few rhizoids and a few archegonia. Following fertilization the zygote produces a new sporophyte generation.

Equisetum

Brief mention should be made of the "horsetails"—hollow, jointed Pteridophytes that are widely distributed and often attract the attention of the traveler and camper. The stems are erect, cylindrical, hollow, and sculptured with vertical grooves and ridges. The leaves are

scale-like in whorls at the nodes. These plants are heavily impregnated with silica and feel very harsh to the touch. The plant as just described is the sporophyte, which in some species occurs in two forms, one much branched and sterile, the other erect, unbranched, and spore-

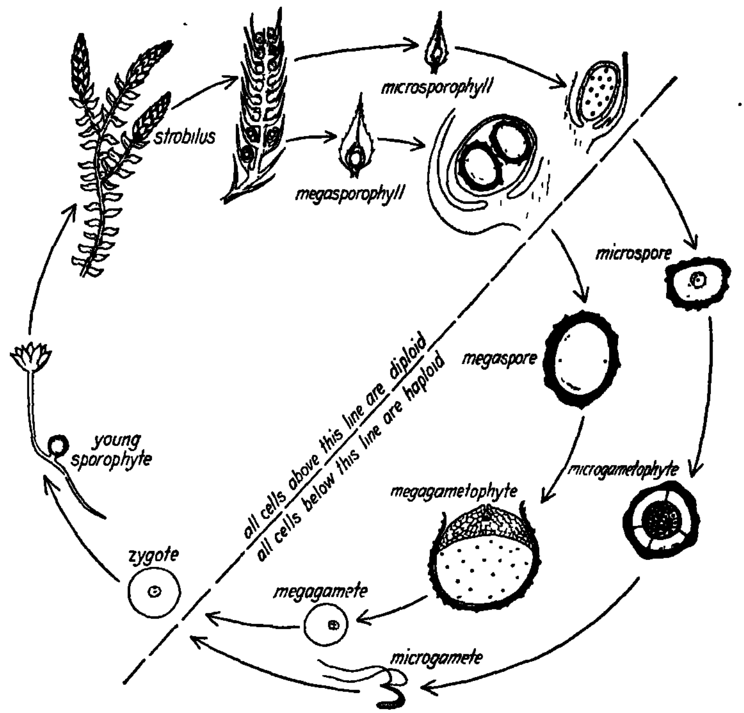


FIG. 254. *Selaginella.* Life history. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc.)

bearing. Both have small, scale-like leaves. Commonly the same perennial rhizomes produce first a crop of fertile branches and then a crop of sterile branches, thus alternating indefinitely.

Each fertile sporophytic shoot bears a definite strobilus at the tip and morphologically only one kind of spore is produced, i.e., all the spores appear microscopically to be of one kind. However, some produce male gametophytes and others female gametophytes, a fact which shows them to be actually different.

The gametophytes in *Equisetum,* as in other Pteridophytes, are

green and very small—generally an eighth to a fourth of an inch long. The male, which is somewhat the smaller, bears a few antheridia, and

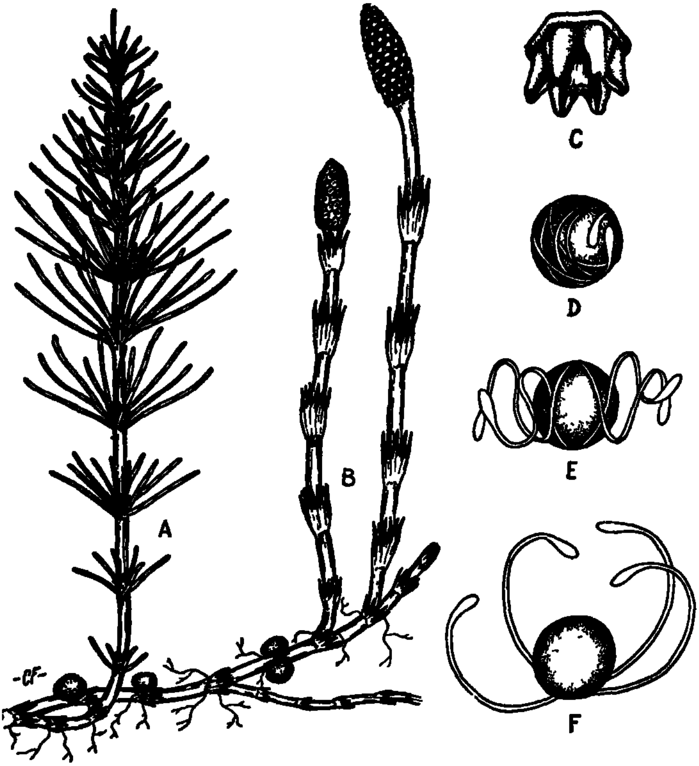


FIG. 255. *Equisetum arvense.* A, sterile shoot; B, fertile shoots producing strobili containing spores; C, spore-bearing portions of strobilus; D, E, F, spores. (From Robbins & Rickett's *Botany,* D. Van Nostrand Company, Inc.)

the female bears a small number of archegonia. These small, inconspicuous gametophytes are rarely seen except by botanical students.

Ages ago tree-like ancestors of our horsetails were among the most conspicuous vegetation of the earth.

THE DOMINANCE OF THE SPOROPHYTE

The thoughtful student has already noted that, as we ascend the scale of plant life from the liverworts, the proportionate size of gameto-

phyte and sporophyte is changing in favor of the latter. In liverworts the gametophyte is many times larger than the sporophyte, in mosses the two are nearly equal in size, while in ferns the sporophyte is very much the larger. It must now be realized that this tendency continues. How far? How small can the gametophyte become? In *Selaginella* it is scarcely visible to the unaided eye, while in the flowering plants it is reduced to microscopic size within the flowers. This tendency is very significant, for the possibilities of development of the sporophyte are very great and have resulted in mighty trees and incomparable flowers,

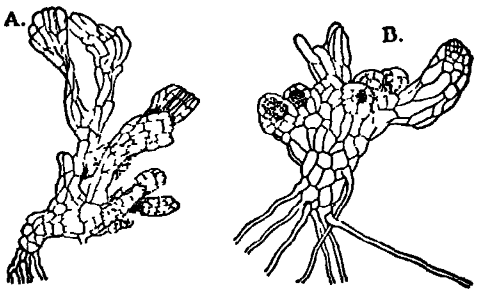


FIG. 256. *Equisetum.* A, female gametophyte; B, male gametophyte. (From Martin's *Botany, with Agricultural Applications,* John Wiley & Sons, Inc.)

while the best the gametophyte has ever achieved is an alga or a humble, leafy moss plant. Furthermore, the sporophyte of the algae seems to be different in character from that of the Bryophytes, Pteridophytes, and Spermatophytes, for there is little to indicate a tendency in it toward dominance over the gametophyte.

Heterospory, as found in certain ferns and in the club-mosses and horsetails, merits careful study; for in the march of evolution toward the flowering plants it represents almost as great an advance over the homospory of the lower forms as does the independence of the fern sporophyte over the dependence of the moss sporophyte.

Relationships of the Pteridophyta

It was once supposed that certain green algae evolved into liverworts, the liverworts into mosses, the mosses into ferns, the ferns into club-mosses, and the club-mosses into seed plants; but deeper study has revealed that the story is not so simple. However, the striking similarity of the sex organs, especially the archegonia, and the character of the

antherozoids suggest a close relationship among these plants, and this idea is supported by the regularity and character of the alternation of generations, which is more obvious than that found in most Thallophytes. Evidence points to a common ancestor for all the Bryophytes

FIG. 257. Composite restoration of the vegetation of the late Paleozoic era, showing giant forms of various Pteridophytes. (From Seward's *Plant Life Through the Ages*, Cambridge University Press.)

and Pteridophytes, probably one similar to a liverwort and evolving from a green alga. Some prehistoric member of the Pteridophytes probably was ancestral to the present seed-bearing plants.

ECONOMIC SIGNIFICANCE

In past ages most of the coal deposits were from ferns, lycopods, and Equisetums, and from the seed ferns, which had attained a gymnosperm structure. Some representatives of all these groups were of gigantic size. The club-mosses or "ground pines" are much prized for Christmas wreaths, and ferns are widely used for the decorative value of their great compound leaves.

Review Questions

1. To what division do the ferns belong?
2. What is the most important advance that the Pteridophyta show over the Bryophyta?
3. What part of the fern is homologous with the thallus of *Marchantia*?
4. Compare the longevity of gametophyte and sporophyte in the fern.
5. How does the sporophyte of the fern obtain its food?
6. How do the relative sizes of gametophyte and sporophyte compare in liverworts, mosses, and ferns?
7. Where are the spores of the fern produced?
8. Describe the gametophyte of a fern.
9. How are the fibrovascular bundles of the fern arranged, as seen in cross-sections?
10. How are the phloem and xylem arranged in each bundle?
11. Give the life history of *Polypodium*.
12. What is the distinction between homospory and heterospory? Name a Pteridophyte illustrating each.
13. Name the kinds of spores produced by *Selaginella*.
14. Where is each produced?
15. Describe: (1) the male gametophyte, and (2) the female gametophyte of *Selaginella*.
16. What portions of (1) the male gametophyte, and (2) the female gametophyte of *Selaginella* are homologous with the thallus of *Marchantia* and the prothallium of the fern?
17. Why is not the leaf of *Selaginella* homologous with the leaf of moss?
18. What is meant by a sporophyll?
19. Give the life history of *Selaginella*.
20. How does the chromosome number of the sporophyte compare with that of the gametophyte?
21. At what stage does the chromosome number become doubled in the fern?
22. At what stages does it become reduced?
23. Describe the appearance of *Equisetum*.
24. Give the economic significance of the Pteridophyta: (1) prehistoric forms, (2) present-day forms.
25. Describe the Pteridophyte vegetation of the earth when at its maximum.

CHAPTER XXIV

SPERMATOPHYTA—SEED PLANTS

The first half of this book dealt almost exclusively with the flowering plants. In those early chapters the subject of reproduction was treated only in a superficial way, for a thorough consideration would have been meaningless before a knowledge of the alternation of generations was obtained from a study of the Phaeophyceae, Bryophyta, and Pteridophyta.

The seed-bearing plants make up the largest, the best-known, the most highly developed, and in some ways the most important division of the plant kingdom.

Gymnosperms

In the Spermatophyta there are but two classes, the Gymnosperms, illustrated by our cone-bearing trees, and the Angiosperms or true flowering plants A more definite distinction between these two classes lies in the fact that the Gymnosperms produce no pistils and therefore no fruits, the seeds being naked, while the Angiosperm seeds are borne within pods, capsules, or other types of fruit. About 500 species of Gymnosperms have been described

Pinus

The lower Gymnosperms are mostly fern-like in appearance and are found in tropical or sub-tropical regions, while the higher Gymnosperms are our familiar pines, spruces, junipers, and related trees growing in temperate and sub-arctic climates. Some of them are gigantic in size—the largest of all living things.

The Sporophyte.—The pine tree is a sporophyte. Its roots, stems, and leaves are made up of cells with 2n chromosomes.

The fibrovascular bundles of the stem are arranged like those of dicotyledonous plants. There is a cambium layer separating the bark, which is mostly phloem, from the wood, which is xylem. The xylem in pine, as in most Gymnosperms, consists almost entirely of tracheids, no vessels (tracheae) being formed. Annual rings of growth are very

conspicuous. The pine also has resin ducts containing "pitch." These ducts are not cells but cylindrical intercellular spaces bounded by cells. They ramify through all parts—roots, stems, and leaves, but in the heart wood they have ceased to function. When a pine tree is wounded the pitch oozes out and helps to protect the exposed surface.

FIG. 258. Isolated tree of the Western Yellow Pine, *Pinus ponderosa.*

The branches of the pine are borne in whorls, a new one usually being produced each year. These must not be confused with nodes, for numerous leaves are produced on the stem between them.

The leaves are needle-shaped and borne in groups of two to five. The number in a sheath aids in distinguishing the species. Thus we have two-needle, three-needle, four-needle, and five-needle pines. The leaves are called "evergreen" because the old ones persist until long after the formation of new ones, so that the tree is never defoliated. The length of time they remain on the tree varies, but it is generally from three to six years.

A cross-section of a leaf shows a thick-walled epidermis with deep-set stomata, a mesophyll densely filled with chloroplasts, and two fibrovascular bundles enclosed in a layer of endodermis.

Pinus, like *Selaginella* and some ferns, is heterosporous, but here specialization has gone further in that the two kinds of spores are produced in separate strobili—both on the same tree in most species.

The staminate, or male, strobili are borne in clusters at the tips of branches. Each strobilus is about one-fourth of an inch long and bears many scales. According to one interpretation each scale is equivalent to a stamen. On the under side of each scale is a pair of microsporangia, or pollen sacs. These are densely packed with microspores which develop into pollen grains. The microspores are one-celled and each has a pair of hollow air sacs or wings, one on either side, formed by inflations in the spore wall. While still in the pollen sac the protoplast of the microspore divides twice. The resulting

four-celled structure with its pair of wings is a pollen grain. After the pollen grains are shed the staminate strobili shrivel and fall off.

The carpellate, or female, strobili are borne on other branches, either singly or in twos or threes. At pollination time they are small,

FIG. 259. Young pine tree showing branches in whorls.

like the staminate strobili or even more slender, and pale green in color. They are less conspicuous, since there are fewer in a cluster (1 to 3) and they are covered with short leaves. On top of each scale in these cones is borne a pair of megasporangia (ovules), each containing a megaspore mother cell, which divides to form four potential megaspores. Only one of these becomes functional, for as it enlarges it crushes the other three and many of the surrounding cells as well. The whole megasporangium with its contents is an ovule.

The tissue covering the megaspore at the micropylar end is called the *nucellus*. A sheath of integument, starting at the base, partly covers

FIG. 260. Leaf clusters from different species of pine. 1, young and 2, old leaf clusters of *Pinus Murrayana;* 3, *Pinus ponderosa;* 4, *Pinus flexilis.*

this and forms a *pollen chamber* which receives the pollen grains. In this pollen chamber a clear liquid is secreted which aids in germination.

The Male Gametophyte.—Pine trees shed their pollen in enormous quantities—veritable yellow clouds that drift away and some-

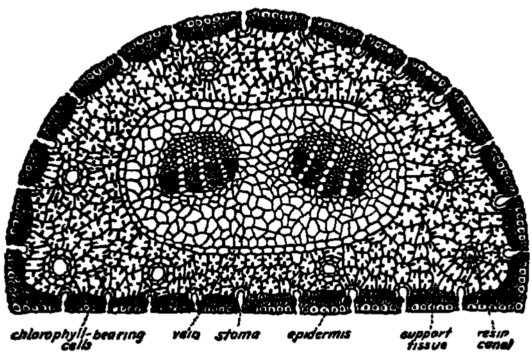


FIG. 261. Cross-section of a pine leaf. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

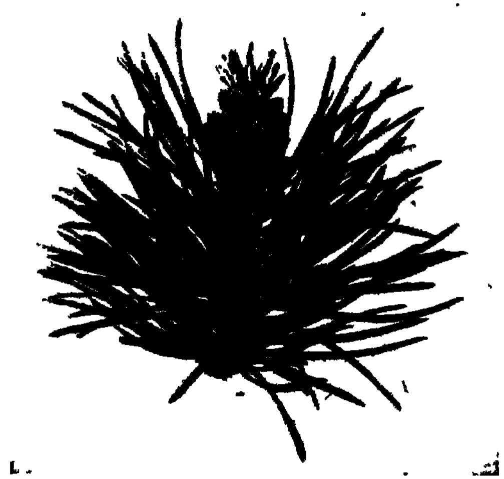


FIG. 262. Lodgepole pine, *Pinus Murrayana*. Staminate strobili.

times produce what lumbermen call "showers of sulfur." Most of the grains are lost, but a very few that happen to fall among the scales of the female cones function in reproduction. They are not male gametes but young male gametophytes. In *Pinus* the mature male gametophyte

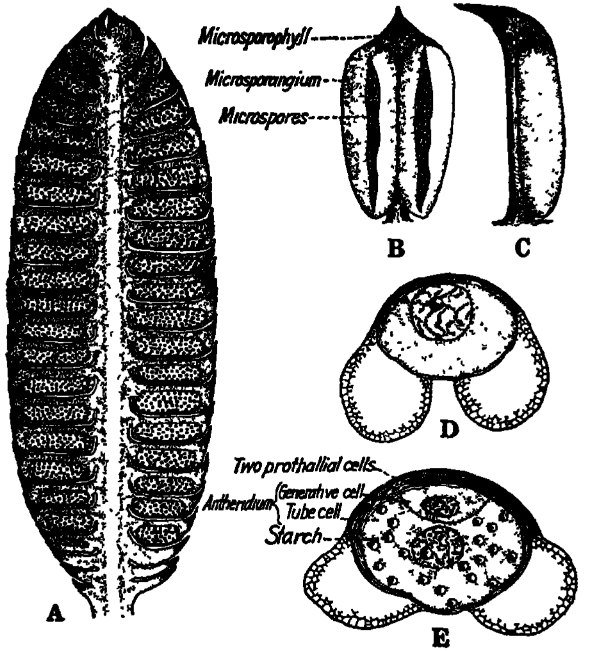


FIG. 263. Austrian pine, *Pinus Laricio*. A, longitudinal section of staminate strobilus; B, scale seen from underneath; C, side view of scale; D, E, microspore developing into pollen grain. (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company, Inc.)

is the germ tube of a pollen grain. The pollen grain starts as a one-celled microspore. While still in the pollen sac of the strobilus this cell divides, and if a pollen grain falls into the pollen chamber of an ovule division is repeated until five cells have formed. In the process of germination the outer wall of the pollen grain is ruptured, and through the breach the germ tube is pushed, covered by the inner wall, which extends and envelops it, thus becoming the tube wall. This germ tube penetrates the nucellus, or wall, of the ovule, a process that requires nearly a year. The mature male gametophyte now consists of the re-

Fig. 264. Lodgepole pine, *Pinus Murrayana,* showing development of ovulate strobili. 1, pair of strobili before pollination; 2, pair of strobili shortly after pollination; 3, pair of strobili one year old; 4, pair of strobili two years old after the seeds have been shed; 5, top view of scale bearing two seeds; 6, single seed with wing.

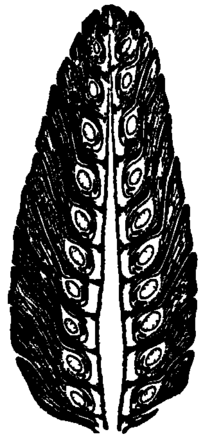


Fig. 265. Longitudinal section of ovulate strobilus of pine at the time of pollination. Diagrammatic. (From Sinnott's *Botany, Principles and Problems,* McGraw-Hill Book Company, Inc.)

mains of two disintegrated *prothallial* cells, still within the pollen grain, and a slender germ tube containing three other cells—a *tube* cell, a *stalk*

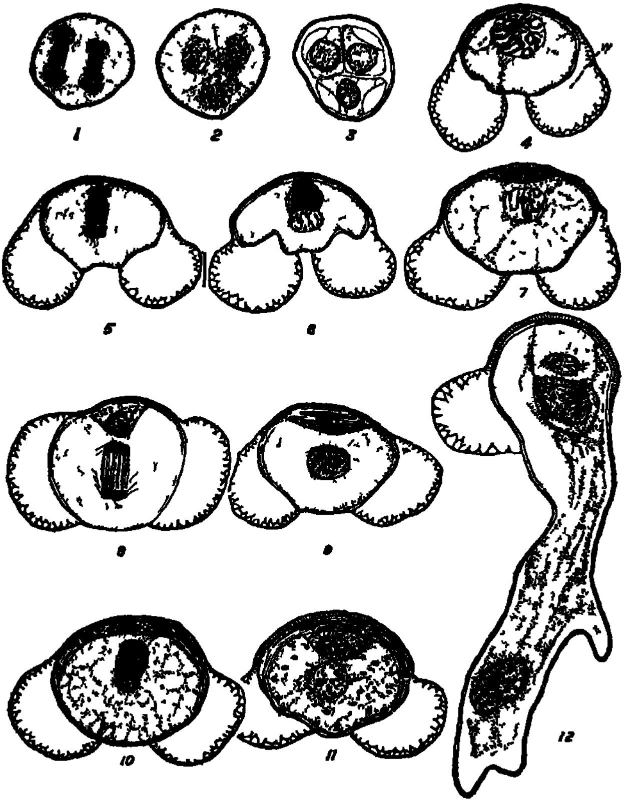


FIG 266 Development of microgametophyte of pine 1 to 4 formation of microspores from mother cell, 5 to 7 formation of pollen grain from microspore, 8 to 12 germination of pollen grain to form microgametophyte (From Coulter and Chamberlain's *Morphology of the Gymnosperms*, University of Chicago Press)

cell, and a *body* cell All have small nuclei except the body cell, which contains two large male gamete nuclei [1] Nearly a year is required for

[1] What is here designated as a body cell with two male nuclei is interpreted by some botanists as two male cells in which the cytoplasm has not separated

the formation of the male gametophyte and its penetration of the nucellus.

The Female Gametophyte.—When first formed the megaspore is one-celled. It is deeply enclosed within the nucellus, where by the fol-

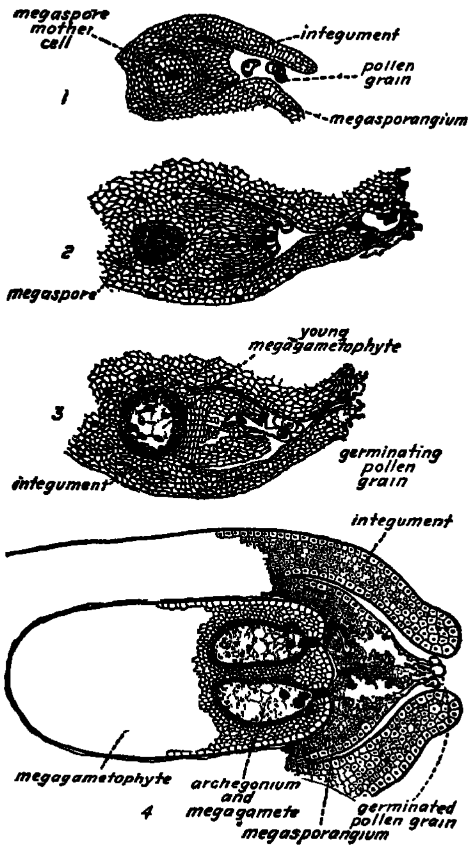


FIG. 267. Development of megagametophyte of pine within an ovule. (From Robbins & Rickett's *Botany*, D. Van Nostrand Company, Inc.)

lowing spring it has developed into a female gametophyte. During this process cell division and growth have taken place until a small oval body has been formed. The mature female gametophyte consists of several hundred vegetative cells and two, or rarely three, archegonia,

each containing a large egg cell. Being hidden from the light, the female gametophyte is whitish in color.

Fertilization.—By the next spring, almost a year after pollination, the pollen tube with its male nuclei has grown through the nucellus. When it reaches the opening of the archegonium, the tip bursts and discharges the gamete nuclei, one of which unites with the egg cell while

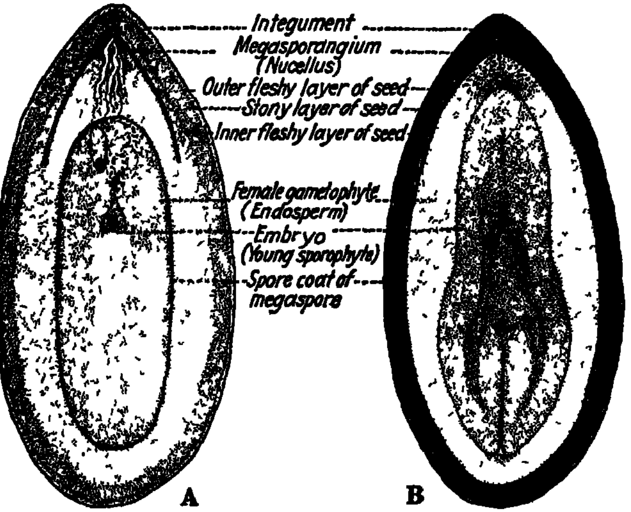


FIG 268. Development of pine seed A, two embryos have started and the suspensors have pressed one of them deep into the endosperm, B, single mature embryo, its mate having failed to develop to maturity (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company, Inc)

the other is absorbed. In this process of gametic union the male and female nuclei lie in contact and each starts to divide. Spireme threads appear and split longitudinally, and each nucleus forms a spindle, the two lying close together and parallel. As soon as the spireme threads break up into chromosomes, the two spindles fuse into one which carries all the chromosomes. Thus the nuclei unite during the mitosis, and the resulting zygote contains two nuclei, each of which has a combination of male and female chromosomes.

Formation of the Seed.—During the year required for the pollen grains to germinate and grow through the nucellus, the vegetative portion of the female gametophyte has enlarged considerably and become

richly stored with food that will serve to nourish the embryo during its development and during the germination of the seed. This structure is now called the *endosperm*.

The zygote undergoes repeated nuclear and cell division, and four of the cells form a *suspensor*, which, by elongation, pushes the remainder of the embryo from its original position in the archegonium deep down into the center of the endosperm where it finishes development. The fully developed embryo is a straight, little sporophyte plant consisting of several cotyledons in a cluster, a rudimentary stem, and a rudimentary root. It is entirely surrounded by the nutritive endosperm. Meanwhile the nucellus has been largely absorbed by the endosperm and forms only a thin layer, while the integument has extended around it to form a seed coat, which becomes hard and brown. In most pines a portion of the cone scale becomes attached to the seed to form a wing. As a rule two naked seeds are found on top of each scale of the female cone.

Seed formation in the pines is a slow process. Pollination takes place in early summer, and fertilization a year later. The seeds mature that autumn, more than a year after pollination, but in some species they remain in the cones for another year or more after maturity.

Life History.—The life history of Gymnosperms is well illustrated by *Pinus*. The sporophyte is a large evergreen tree. It bears two kinds of strobili—staminate strobili with microspores and carpellate strobili with megaspores. The microspores develop into pollen grains, which fall into the pollen chambers of the ovules, germinate, and penetrate the nucellus, producing five cells, one of which contains two male nuclei. The megaspore develops into an oval, many-celled structure with two or three archegonia. A pollen tube discharges its male nuclei into the archegonium and one of them unites with the egg cell. The zygote thus formed develops into an embryo, the vegetative cells of the female gametophyte develop into a nutritive endosperm, and the integument forms a seed coat. The seed lies dormant for a time and then develops into a sporophytic pine tree.

Comparison of Selaginella and Pinus.—*Pinus* shows several points of advancement over *Selaginella*. (1) Both are heterosporous, but *Selaginella* produces both microspores and megaspores in the same strobilus while *Pinus* has two kinds of strobili. (2) In *Selaginella* the male gametes are motile like those of its aquatic ancestors, but in *Pinus* the male gametes are nuclei in the tip of a pollen tube, a more perfect adaptation to the terrestrial habitat. (3) In *Selaginella* the megaspore containing the female gametophyte falls to the ground for

further development, but in *Pinus* it remains in the ovule on the tree. (4) The female gametophyte of *Pinus* is smaller and simpler, without rhizoids. (5) In *Selaginella* the embryo develops without interruption into a sporophytic plant, but in *Pinus* it becomes dormant, and, with its endosperm, integument, wing, etc., becomes a seed.

Other Gymnosperms

Gymnosperms once formed the dominant vegetation of the earth. Altogether seven orders of Gymnosperms are known. Three of these; Bennettitales, Cordaitales, and Cycadofilicales, are extinct and are represented only by their fossils. Two others, Gnetales and Ginkgoales, are quite rare, the former containing three small genera and the latter but one with a single species—the beautiful maidenhair tree of China. Of the remaining two the Coniferales make up the great evergreen forests of temperate and colder regions, especially in the northern hemisphere, while the Cycadales, many of them resembling coarse ferns but producing seeds, are chiefly confined to the tropics and sub-tropics.

In the Ginkgoales and the Cycadales the male gametes are motile with many cilia. They somewhat resemble those of the ferns but are even more elaborate.

Economic Significance

Of great commercial value is the lumber from coniferous forests—pine, hemlock, fir, spruce, cedar, etc. Fuel, turpentine, and resins are other contributions from the conifers. These evergreen trees, with their dark-green foliage, do much to beautify the landscape, either as massive forests or as individual trees transplanted and propagated for their decorative value. The "big trees" of California are unsurpassed for their grandeur.

Angiosperms

The Angiosperms are the true flowering plants. Much has been said in earlier chapters about their morphology and physiology, but a closer study of their reproduction is necessary. Many botanists, but not all, interpret the flower as a highly specialized strobilus in which the lower scales have ceased to be sporophylls and have become sepals and petals, while the upper ones have evolved into stamens and carpels. Very few fossils have ever been found that help to solve the problem as to how flowers evolved from strobili.

The structural differences between monocotyledons and dicotyledons,

especially with reference to the fibrovascular systems in stems and leaves of the sporophyte, have been discussed in earlier chapters. In their gametophytes, however, there is no distinguishing difference.

FIG. 269. Easter lily, a representative monocotyledonous plant. The floral parts tend to be in multiples of three.

Lilium

The genus *Lilium* is representative of the simpler monocotyledonous Angiosperms. Here, as in the Gymnosperms, the entire plant visible to the unaided eye is the sporophyte.

The Male Gametophyte.—Pollen grains in the anthers of *Lilium* are at first one-celled and uninucleate. Nuclear division soon takes

place, however, and the cell then divides into two, a tube cell and a generative cell separated only by their plasma membranes. Shortly after

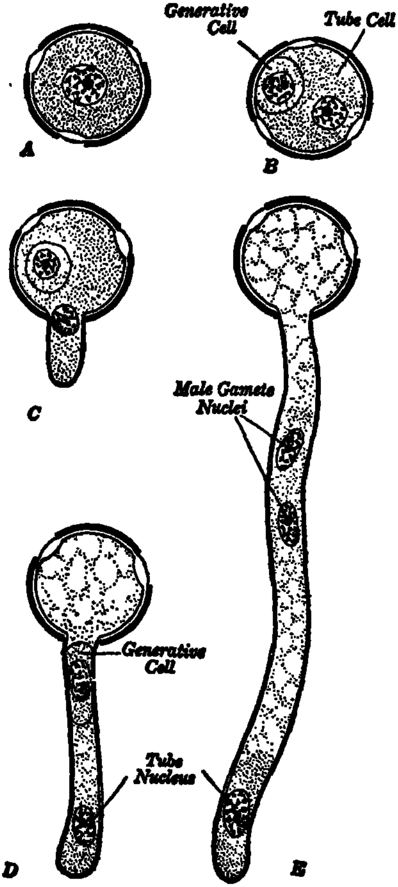


FIG. 270. Development of the microgametophyte in an Angiosperm. A, microspore; B, pollen grain developed from microspore; C to E, germination of pollen grain to form microgametophyte. (From Smith, Overton, et al., *Textbook of General Botany,* The Macmillan Company.)

reaching the stigma the generative nucleus divides and forms two male gamete nuclei. The germ tube then pushes down into the stigma and style. The male gametophyte thus consists of but two cells with three

nuclei, two of them gamete nuclei. In some Angiosperms nuclear division in the generative cell is followed by cell division, thus forming two male gamete cells.

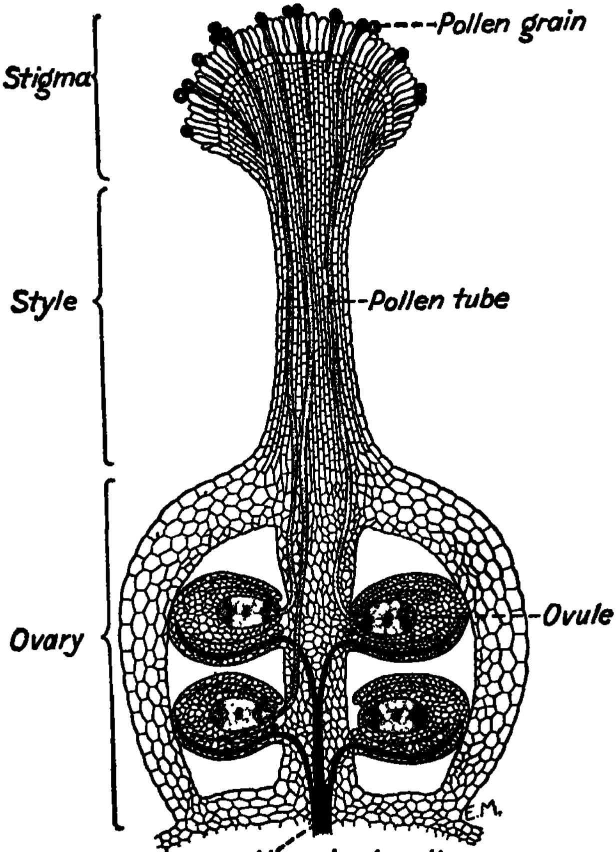


FIG. 271. Longitudinal section of a pistil at the time of fertilization. Diagrammatic.

The Female Gametophyte.—In the production of the female gametophyte considerable variation is found among the different species of Angiosperms. As Lilium differs markedly from most Angiosperms in

the formation of the female gametophyte, the commoner method will be given here instead.

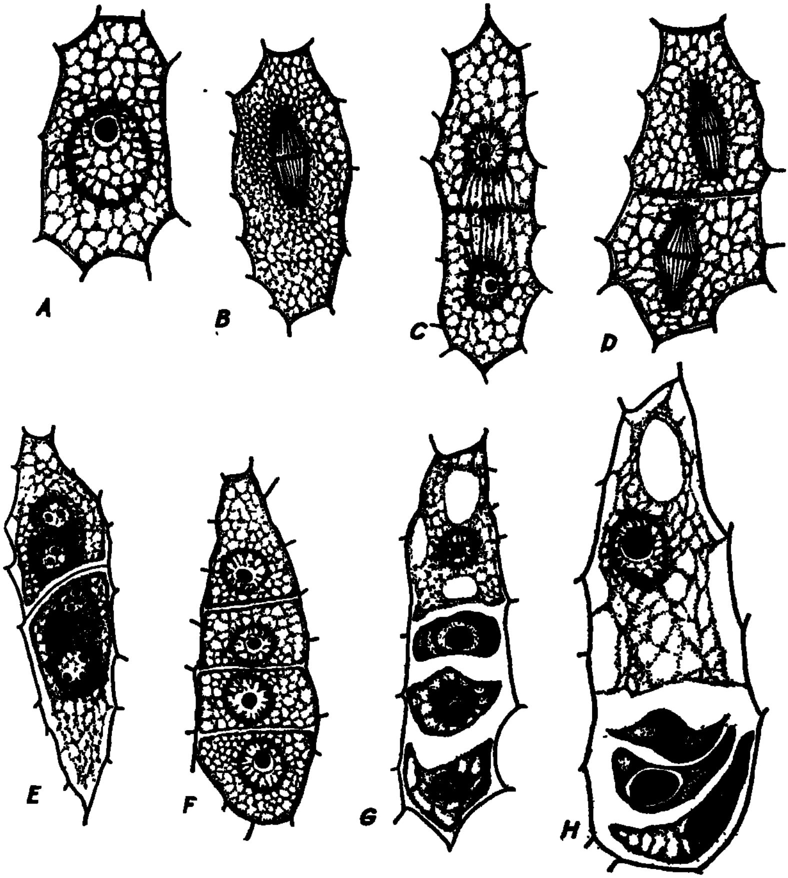


FIG. 272. Development of the megaspores in *Carex*. A, megaspore mother cell within the ovule. B to F, division of mother cell to form four megaspores. G, H, degeneration of 3 megaspores leaving one functional. (Reprinted by permission from *Botany* by Hill, Overholts and Popp, published by McGraw-Hill Book Co., Inc.)

In the method characteristic of most Angiosperms the procedure is as follows: Deep within the nucellus of the ovule a megaspore mother cell divides twice to form four potential megaspores, but only one of

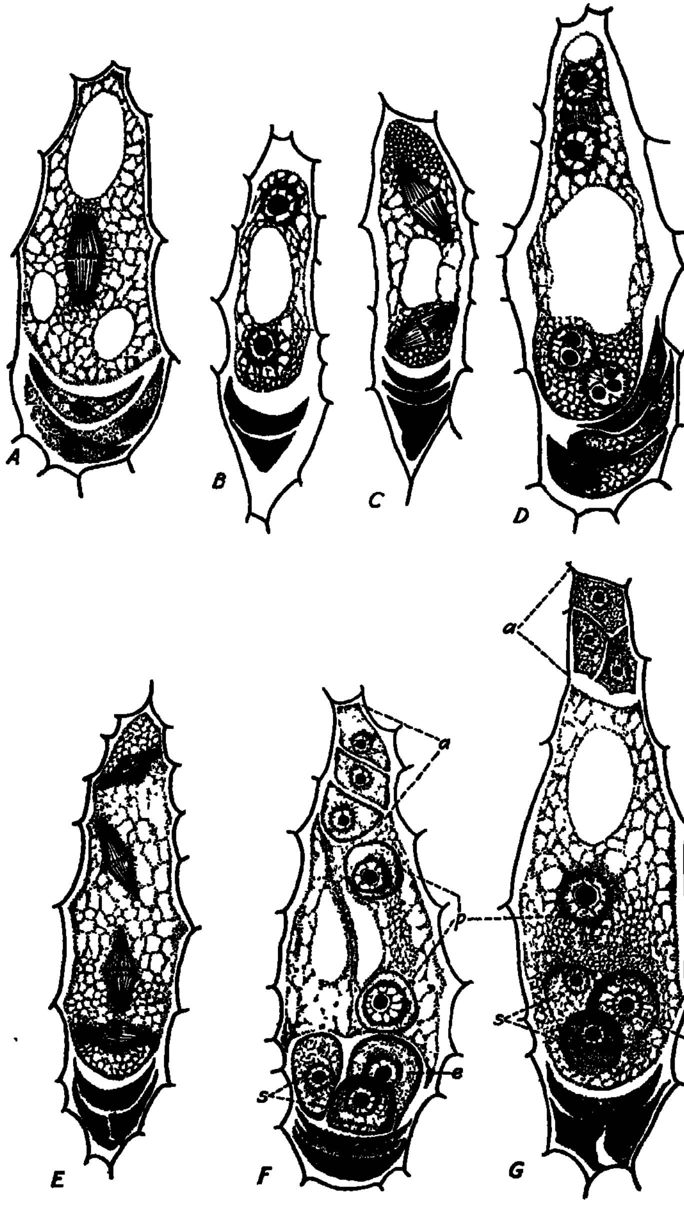


FIG. 273. Development of the female gametophyte of *Carex* from the megaspore. A to F, nuclear division to form the eight typical nuclei of the female gametophyte in Angiosperms. In G the two polar nuclei have united. Egg nucleus, e. (Reprinted by permission from *Botany* by Hill, Overholts and Popp, published by McGraw-Hill Book Co., Inc.)

these becomes functional. The others fail to develop and soon shrivel away. The mother cell has 2n chromosomes and the megaspore has n chromosomes. In its development into a female gametophyte the megaspore elongates, and its nucleus divides to form eight nuclei, six of which become surrounded by new cell membranes. Three of these, the *antipodal* cells, are at the end of the gametophyte opposite the micropyle of the ovule and have no known function. Three others, the egg and two *synergids,* are at the micropylar end. The synergids are supposed to serve as "helpers" to the egg. In the middle of the cell from which

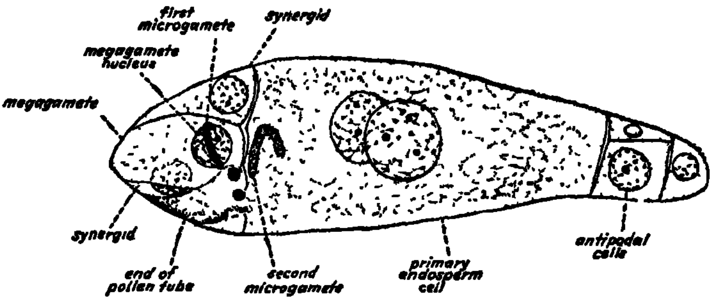


FIG. 274. Fertilization in an Angiosperm. (From Smith, Overton, et al., *Textbook of General Botany,* The Macmillan Company.)

these six new ones formed are the two *polar* nuclei. This female gametophyte is often called the *embryo-sac.* The egg is now ready for fertilization.

Fertilization.—The tip of the pollen tube enters the micropyle and discharges its two gamete nuclei into the embryo-sac. One of these unites with the egg nucleus and the other with the two polar nuclei. As the second male nucleus and the two polar nuclei each have n chromosomes and all three unite into one, the product of this fusion, the *primary endosperm nucleus,* has 3n chromosomes.

Development of the Seed.—Seed formation takes place by a combination of several processes that go on more or less simultaneously. (1) An embryonic sporophyte plant forms from the zygote. (2) The fertilized embryo-sac, with its 3n primary endosperm nucleus, undergoes nuclear and cell division and thus forms the endosperm, which is the conspicuous food storage region of corn, wheat, and many other plants. In some species, such as sunflower, bean, and squash, the developing embryo absorbs the endosperm so that in the ripe seed the food is stored

in the cotyledons of the embryo instead. (3) Integuments, generally two, starting from the basal half of the ovule, extend around it except for the micropylar opening, which may remain partly open. Thus the

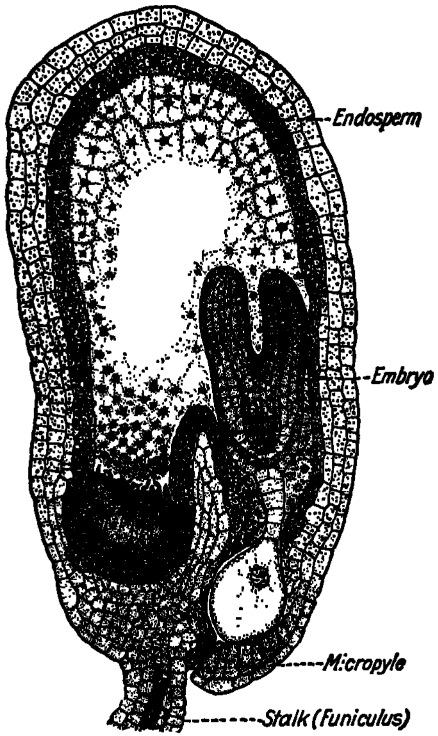


FIG. 275. Ovule of shepherd's purse containing an embryo and an endosperm. (From Chamberlain's *Elements of Plant Science*, McGraw-Hill Book Company, Inc.)

ovule, or megasporangium, with its contained embryo and endosperm, becomes a seed.

At the same time the ovary wall, made up of one or more carpels, develops into the fruit enclosing the seeds.

Gametophyte versus Sporophyte

Already it has been pointed out that as plants ascend the scale of life from the liverworts, the gametophyte becomes progressively smaller and

simpler and the sporophyte progressively larger and more complex The climax of this tendency is reached in the Angiosperms, where the male gametophyte is but a germ tube with two, or sometimes three, cells and the female gametophyte is but seven cells (one with two nuclei) with no archegonium Is it theoretically possible that these gametophytes could be reduced still further? Conceivably the microspore with its n chromosomes and the megaspore with its n chromosomes might ultimately come to function as gametes without further nuclear or cell division

In contrast with the degenerated gametophytes, the sporophyte has made the amazing development that distinguishes the orchid from the liverwort Is it theoretically possible for the sporophyte to progress still further? Probably so, but man can only guess the direction that such a development might take

RELATIONSHIPS OF THE SPERMATOPHYTA

There seems little doubt that the seed plants evolved from the Pteridophytes, probably the heterosporous ferns or their immediate ancestors The Angiosperms are generally conceded to be higher than the Gymnosperms and to have evolved from them into the most highly developed forms of plant life There are nearly 200,000 species of Angiosperms, no two exactly alike

REVIEW QUESTIONS

1 Name the four divisions of the plant kingdom
2 Give the generic and specific names of a plant in each division
3 What appears to be the evolutionary origin of each division?
4 Name the two classes of Spermatophyta
5 What is the most important distinction between these two classes?
6 Where are the microspores of the pine borne?
7 When a microspore germinates what does it produce?
8 Describe the male gametophyte of pine
9 Where are the megaspores borne?
10 Describe the formation of the female gametophyte from the megaspore.
11 Describe the female gametophyte of the pine
12 Where is it found?
13 Trace the reduction in the female gametophyte of the Spermatophyta, describing its appearance in Gymnosperms and Angiosperms, and indicating to what extent it could be further reduced
14 As we ascend the scale of plant life from the Chlorophyceae to the Angiospermae, where does the male gamete cease to be motile?

15. Explain the lag in the change from motile gametes to non-motile gametes as plants took up a terrestrial habit.
16. Which of the following belong to the gametophyte generation and which to the sporophyte generation: (1) leaf of apple, (2) protonema of moss, (3) root of fern, (4) leaf of *Selaginella*, (5) spore of moss, (6) antherozoid of *Marchantia*, (7) leaf of moss, (8) prothallium of fern, (9) rhizoid of *Marchantia*, (10) seed of pine?
17. How are the fibrovascular bundles of the pine stem arranged?
18. What part of the flower is the microsporangium? The megasporangium?
19. What part of a flower develops into each of the following (1) stem of fruit, (2) fruit, (3) seed, (4) embryo, (5) endosperm?
20. Describe the sporophyte of a lily.
21. Give the life history of pine or lily.
22. Define: (1) carpel, (2) heterospory, (3) embryo-sac, (4) ovule, (5) embryo, (6) nucellus
23. Some extinct fern-like plants produced seeds but no flowers They have been called "seed ferns." Should they properly be classed as Pteridophytes or Gymnosperms?
24. What morphological structures indicate a close relationship between liverworts, mosses, ferns, club mosses, horsetails, and pines?
25. Why is a well-developed fibrovascular system so much more necessary in a spermatophyte than in a brown alga of the same size?
26. Describe in as much detail as you can the changes that would have to take place in *Selaginella* to make it become a Gymnosperm

PART SEVEN

PLANTS PAST AND PRESENT

CHAPTER XXV

THE ORIGIN OF PLANT GROUPS

There exist on the earth today hundreds of thousands of plant species and hundreds of thousands of animal species. In ages gone untold numbers of other species have flourished for a time and disappeared, failing to become adapted to a changed and hostile environment. We live with the survivors.

What has been the origin of all these groups? Among educated people it is generally accepted as a fact that some species appeared on the earth much later than others, that the more recent groups are the higher ones in the scale of life, and that these higher forms had ancestors more simple than themselves.

Botanists and zoologists face profoundly difficult and interesting problems in their attempts to trace the origin of life in its different forms. To mention a few of them: (1) Where and when did the first form of life appear? (2) Did life originate from the materials of the earth only once or more than once? (3) What caused it to come into existence? (4) What was the first living thing like?

In the present state of our knowledge it would be presumptuous to attempt final answers to any of these questions, but a few comments will show the trend of thought. It is generally agreed that life first appeared in shallow sea water along the shore or among islands or shoals. As a result of unknown forces, certain elements or simple compounds combined into proteins and other organic substances. Whether this happened once or many times is problematical. Had it occurred at intervals a hundred times during a million years we would have no way of knowing it. We find no evidence of recent repetitions of such a phenomenon, but the necessary environmental conditions may no longer exist. Furthermore, it is not certain that we would detect such simple living material if it were again to appear in small quantity in our midst.

It seems a safe conclusion that the first form of life was more simple than any that we now recognize. Perhaps it was not even cellular in structure, for cells as we know them, with their differentiation into

cytoplasm, membranes, nuclei, etc., seem to be the products of evolution. Almost certainly it did not possess chlorophyll, which appears to be a later acquisition. That two things as complex as cytoplasm and chlorophyll should be formed together, simultaneously, out of inorganic materials is extremely unlikely. The alternative is for one to have been formed and then the other, probably with the aid of the first. Chlorophyll cannot function in the absence of cytoplasm, nor is it necessary for the production of cytoplasm, and it quickly breaks down in the presence of light and moisture if removed from cytoplasm. Therefore it could hardly have been the first to appear. On the other hand, if cytoplasm were formed first and could live, grow, and reproduce without chlorophyll for even so much as a year, it might be expected to do so for a much longer time. The first life could not have been saprophytic or *parasitic, for at that time there was no organic matter for it to live* on. We must, then, be satisfied with the conception of an undifferentiated protoplasm that had the power of obtaining energy by the oxidation of simple substances such as sulfur, hydrogen sulfide, hydrogen, ammonia, or carbon monoxide, and that was capable of reproducing itself. The nearest we now have to such a form of life is a group of the autotrophic bacteria—those that do not require organic food and that do not have well-developed nuclei. Doubtless the first living material was morphologically even simpler than they are. It is generally presumed that plants appeared before animals, but in the beginning life was probably too simple to be designated either as plant or as animal.

There are different methods of estimating the time since life first appeared on the earth, and these methods yield somewhat different results. Some place the time at 500,000,000 years; others at about twice that many.

The Explanation of Evolution

The foregoing is but suggestive speculation. Equally interesting and more profitable has been the study of how one group of living things evolved from another, and how the characters of an individual are made to reappear in its offspring.

Two Great Foundation Stones.—The possibilities of organic evolution rest on two great fundamental principles, both of which are prominent in the original works of Darwin. These are (1) the tendency of offspring to show variations from their parents and to transmit these variations to their offspring in turn, and (2) the greater likelihood that

those individuals best fitted to cope with their environment will survive long enough to reproduce.

Variation.—The offspring is not always exactly like the parent in every respect. In other words, there is a tendency for the offspring to vary in some particular from the parent. The variation may be very

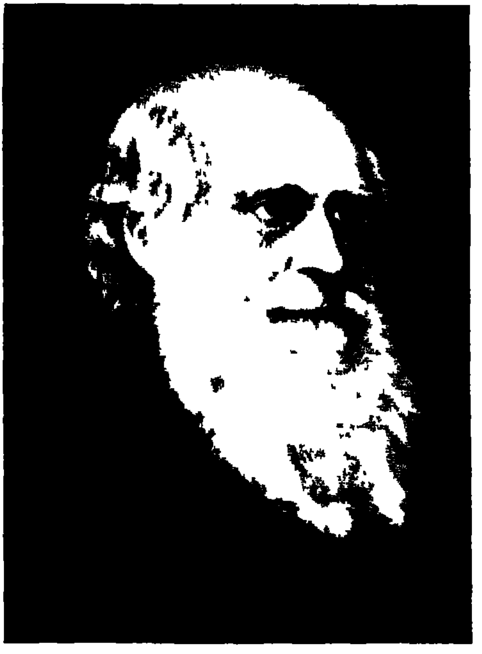


FIG. 276. Charles Darwin (1809-1882). First great exponent of the idea that existing species have arisen by evolution. (From Smith, Overton, et al., *Textbook of General Botany,* The Macmillan Company.)

slight; it may be too little for us to detect. Thousands of generations may appear with practically no variation; there is more variation in some groups than in others; but the tendency to variation exists and we have all seen it in both plants and animals.

Some kinds of variation are heritable and some are not. The offspring may differ in some respect from the parent, but its offspring in turn may perpetuate this variation or it may return to the original condition. It is obvious that only the heritable variations contribute to evolution.

The nature and direction that variation will take cannot be predicted. It must not be supposed that it will always result in the betterment of the race. For convenience we may say that the variation will be (1) beneficial to the race, (2) detrimental to the race, or (3) of no influence whatever on the welfare of the race. The important things to remember now are that many variations occur and that some of these variations are inherited. If such were not the case there could be no evolution.

Survival of the Fittest.—Darwin realized that not every variation is of a nature to make the offspring better suited to meet the problems of life. He reasoned that some would enable the plant or animal to cope more successfully with its environment and thereby increase its chances of surviving to produce offspring, while others would be of a kind to decrease its fitness for its surroundings and thus make it less likely to survive.

This principle of the survival of the fittest is quite generally accepted. It is *not* possible, however, to list the desirable traits on the one hand and the undesirable ones on the other, for much depends on the character of the environment. If, for example, a plant were living in a region rather too wet for its best welfare, variations toward a hydrophytic character would favor its chances for survival. If, however, after it had made considerable progress toward becoming a hydrophyte, climatic changes should set in and the region become arid, the very characters that once fitted the plant for survival would tend toward its destruction. There is little doubt that many plant and animal lines have been exterminated because of too great specialization in some one direction when a change of environment made this specialization disastrous.

Several theories have been proposed to account for the origin of groups by evolution. All of them accept the tendency to variation as the *dynamic* principle that results in evolution, and the survival of the fittest as the *guiding* principle that determines the direction that evolution will take. Differences of opinion center chiefly around five questions: (1) What stimulates or causes variation to occur? (2) What determines the character of the variation that may occur? (3) How great are the variations that may occur between one generation and the next? (4) Does a given type of variation tend to be repeated in successive generations and thereby become *cumulative?* (5) Which variations are heritable and which are not? In efforts to solve these questions various theories have been offered. A few of these have considerable merit, but no one of them is wholly satisfying.

Theories of Evolution

It is of great theoretical and practical interest to try to account for the evolutionary changes that have resulted in the production of higher animals and higher plants. The processes of evolution must not be thought of as having served their purposes and ceased to operate; there is no doubt that they are still going on and will continue into the indefinite future.

Early in the nineteenth century two theories of inheritance were set forth, which, if their authors had had greater astuteness and vision, either would never have been proposed or would have been developed into theories of the evolutionary origin of species antedating Darwin's by a half century. They have little acceptance among botanists today, but they sound so plausible to those who are uninformed in this field that they merit brief comment.

Variations from Environmental Influence.—A French naturalist, August de St. Hilaire, noted that environmental conditions cause variations to take place during the development of an individual and proposed the theory that if a race is continuously subjected to this environment these variations will become permanently established. If of a beneficial character they will result in an adaptation of the race to its environment. If of a harmful character they will tend towards its extermination. The weakness of St. Hilaire's theory is that the variations that take place in an individual during its lifetime and are due to environmental conditions are not heritable.

Variations from Use and Disuse.—Jean Baptiste Lamarck, a contemporary of St. Hilaire, set forth a much better-known theory somewhat similar in character. Lamarck based his theory on the well-known phenomenon that certain organs develop in the individual through use and degenerate from lack of use. He reasoned that environmental conditions may bring about either increase or decrease in the use of an organ and that in this way living things adapt themselves to their environment and even change into new species. The weakness of Lamarck's theory lies in the lack of evidence that variations in the individual caused by use or disuse of an organ are inherited.

Darwin's Theory of Origin of Species by Natural Selection.—Prior to the time of Darwin it was generally assumed that each species was created in its existing form, although a number of people had already expressed the idea that organic evolution takes place. Darwin

found evidence that led him to the conclusion that species have originated from other species which were in most cases simpler than those derived from them. The three main facts used by Darwin to support his theory of evolution are: (1) the tendency to overproduction, (2) the tendency to variation, and (3) the survival of the fittest. Darwin was of a mathematical turn of mind and was impressed with the fact that if every seed produced a plant which in turn lived to produce seed this increase could not continue indefinitely, for the earth could provide neither sustenance nor space for the resulting offspring. Darwin took into consideration all factors of the environment, but these two, food supply and crowding, he particularly emphasized.

Darwin conceived of the variation of an individual from its parents as being very minute but of frequent occurrence. This part of his theory has received the most criticism. The chief exceptions taken to his explanation are (1) that he overrated the heritability of the variations that take place in the individual, although he did not regard all variations as heritable; and (2) that the variations as Darwin conceived of them are so minute that they could not in any one generation be a determining factor in the survival of a plant or an animal.

Orthogenesis.—The theory of orthogenesis is not the product of any one man. It presupposes that when variation in a given direction sets in, it persists in that direction and increases, generation after generation, until the accumulated variation has become sufficient in amount either to aid in the survival of that line or to operate towards its destruction. Suppose, for example, variation in a plant with primitive leaves took the form of an increase of chlorophyll in the cells of the upper half; by the principle of orthogenesis the leaves in each successive generation would become more and more specialized until a definite palisade layer was formed. If this theory of orthogenesis is accepted it greatly strengthens Darwin's explanation of evolution through minute variations and also the mutation theory now to be discussed. Indeed orthogenesis is almost essential to the explanation of evolution and deserves most thorough investigation.

De Vries' Mutation Theory.—The most recent of the great theories of evolution, set forth in 1901, is that of Hugo de Vries, a great botanist of Holland. In studying certain species of evening primroses, particularly *Oenothera Lamarckiana,* he obtained, in a single generation, plants sufficiently different from the parents to be classed as a new species. These sudden and striking departures from the parent characters were suggestive of the "sports" noted by Darwin but considered by

him to be of such rare occurrence that they were not significant as an explanation of evolution. De Vries applied the term *mutants* to the new species arising as variants from *Oenothera Lamarckiana*, and their sudden origin he called *mutation*. It will be noted that the mutations of

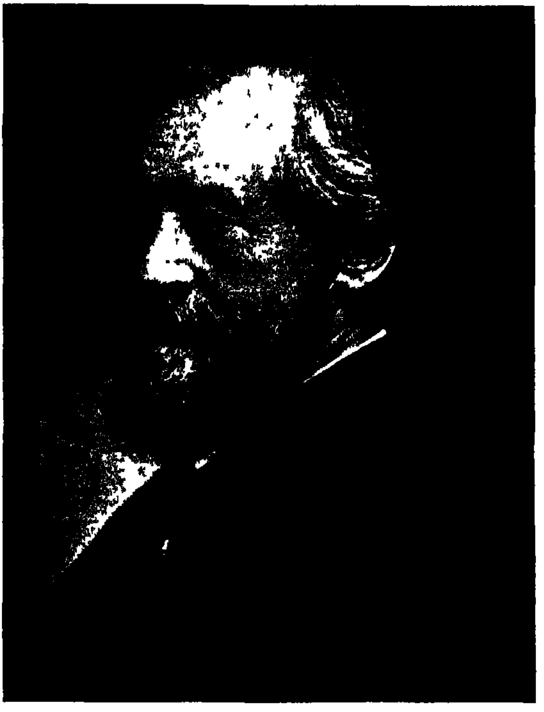


FIG. 277. Hugo de Vries. Great botanist of Holland and author of the mutation theory of evolution. (From Geo. H. Shull, *Journal of Heredity*, Volume 24.)

de Vries show much larger degrees of variation than those postulated by Darwin, large enough, in the opinion of de Vries, to be of significance in making plants better adapted or less well adapted to cope with their environment. It has been objected that mutations are of too rare occurrence to account for all that has taken place by evolution, but when we consider that we have been studying them less than half a century while evolution has been going on for perhaps a billion years, this criticism is hardly justified, particularly if orthogenesis can be shown

to accentuate the mutations that occur. The theory now has a very wide acceptance.

It should be realized that the theories of Darwin and those of de Vries have this in common: that they conceive organic evolution to be the result of heritable variations of offspring from the characters of the

FIG. 278. A, *Oenothera Lamarckiana*, with 14 chromosomes; B, *O. gigas*, a mutant with 28 chromosomes. (From Smith, Overton, et al., *Textbook of General Botany*, The Macmillan Company, after de Vries.)

parent, and that de Vries' conception is, in reality, a modification of Darwin's. The two are not necessarily incompatible, for it is conceivable that some progress in evolution may have been made by the one method and some by the other, and that there may be gradations in the size of the steps of variation between those conceived of by Darwin and those observed by de Vries. Furthermore, orthogenesis, if it is a fact, increases the accomplishment of evolution by variation regardless of the amount of the variation.

Cytological Observations.—Since the chromatin of the nuclei largely determines the characteristics of an individual and since dif-

ferent characters are governed by different chromatin bodies, it is logical to suppose that variations in traits will be accompanied by variations in chromatin structure It may even be inferred that if the chromatin complex of reproductive cells varies from that of the parent cells which produced them, the resulting offspring will be correspondingly different Actual observations confirm this theory After male and female chromosomes have conjugated (see page 390), their separation is sometimes imperfect One of the chromosome pair, as they separate, may take some chromatin belonging to its mate Indeed, one daughter nucleus may receive more than its quota of chromosomes, which will result in a changed number in the offspring It has, in fact, been shown that one of de Vries' mutants of the evening primrose has doubled the chromosome number of the parent species, i e, the diploid number in the parent is fourteen, but that of the giant mutant is twenty-eight.

These cytological discoveries open up a magnificent field for research into the causes of variation Among other things it has been shown that radium rays and certain chemicals stimulate variations of the kind just described, and thus the environment may be a direct factor in producing new forms of life

Laws Governing Heredity and Variation

More conclusive than the theories offered to account for the known facts of evolution are certain laws that determine the way in which *traits of the parent reappear in the offspring* For convenience this is called the inheritance of parental traits [1] It has been a subject of speculation for centuries, but because there was a lack of any definite information on the subject, and because attention was focused too much on the complicated subject of inheritance in the human race, little progress was made, and some incorrect assumptions received general acceptance.

It was known that in animals the traits of both parents tended to reappear in the offspring It was assumed that, for the most part, all the traits of a parent were inherited *collectively,* not as ***unit*** traits Where the parents differed from each other it was assumed that the

[1] Strictly speaking, a plant inherits from its parents a bit of protoplasm to start life with rather than characters, traits, or tendencies, these qualities being expressions of the protoplasm that has been inherited For clarity, however, and to avoid a repetition of awkward roundabout statements, the time-honored method of expression will here be retained

offspring would be intermediate between the two, although plenty of exceptions were observed.

The Work of Mendel.—Much of this careless assumption was set aside by the precise experiments of an Austrian monk, Gregor Johann

FIG. 279. Gregor Johann Mendel (1822-1884). One of the first to use exact methods in studying inheritance, and discoverer of important laws of inheritance. (From Smith, Overton, et al., *Textbook of General Botany*, The Macmillan Company.)

Mendel. Working in his monastery garden at Brunn, he carried on systematic breeding work with garden peas. Using pure strains with fixed characters, he first cross-pollinated them and then in subsequent years allowed self-pollination to take place in the offspring. The varieties of peas that Mendel used differed in several respects, including height of the plants, roughness of the seeds, and color of the cotyledons. One

of the laws brought out by Mendel's experiments, supplemented by later investigations, is that of *unit characters*—namely, that each character is

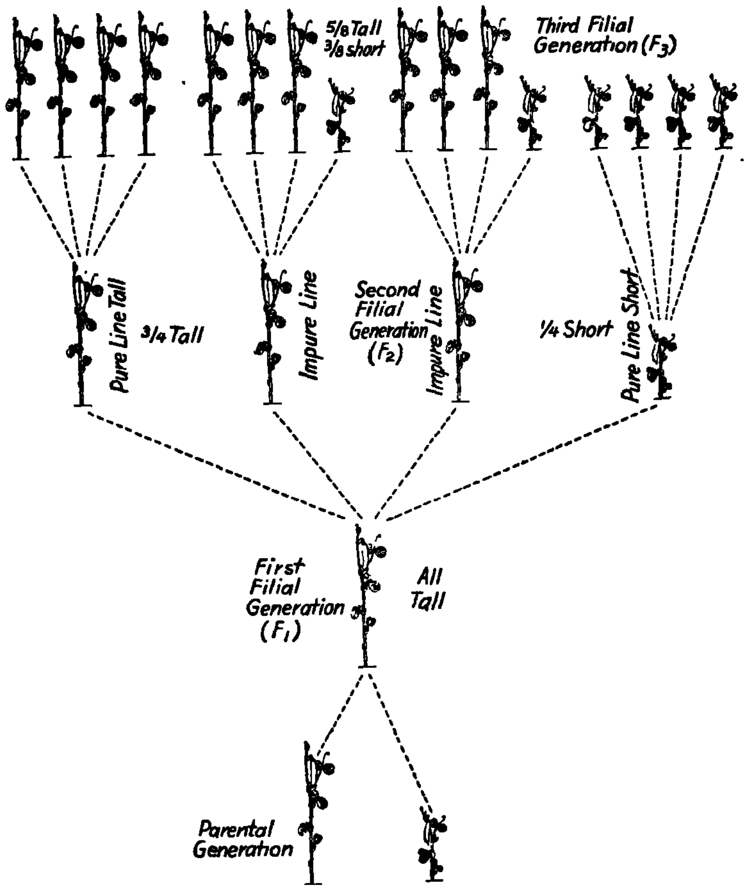


FIG. 280. Diagram illustrating Mendel's law as applied to tall and dwarf peas. In this case tallness is dominant and shortness is recessive.

inherited separately from the others, except where two or more are linked together in a definite way.

Of equal significance is the way in which any given character reappears in the offspring. Tall and dwarf plants will serve as an example.

A pair of traits such as tallness and dwarfness, that are contrasting in character, are known as *allelomorphs*. Mendel pollinated flowers of a tall variety with pollen from a dwarf variety and vice versa. In both cases the result was the same. The seeds derived from this cross and planted the next season produced vines all of which were tall. This is called the *first hybrid* generation, or *first filial* generation, and is designated as F_1. The plants of this F_1 generation were allowed to self-pollinate and produce seed. The next season the F_2 generation was grown from these seeds. In it about three-fourths of the plants were tall and about one-fourth were short. Mendel called the allelomorph that appeared in the F_1 generation *dominant* and the other, which did not appear until the F_2 generation, *recessive*. In this case tallness is dominant and dwarfness recessive. The dominant merely suppresses the recessive without destroying it.

The following season seeds from both the tall and the dwarf vines of the F_2 generation were planted and self-pollinated. In the resulting F_3 generation all the seeds from the short vines produced short vines but those from the tall vines again yielded some tall plants and some short ones. It will be well to go back to the F_2 generation and sum it up in this way. One-fourth of the plants of this generation are pure line for dwarfness and will continue to produce dwarf plants through indefinite future generations. One-fourth are pure line for tallness and will continue to produce tall plants through indefinite generations. The remaining half, all of which are tall in the F_2 generation, are *hybrids* and yield dwarf and tall plants in the proportion of three tall to one short. In each successive generation the distribution of the offspring of the tall *hybrids* as just given will be repeated.

Mendel conducted similar experiments with varieties of peas showing other contrasting characters and obtained essentially the same results. Crosses between varieties differing in one character only, such as stature for example, result in *monohybrids*. Crosses between varieties differing in two characters, such as stature and color of cotyledons, result in *dihybrids*.

It should be said here that one cannot with certainty predict in advance whether a given character will be dominant or recessive, as this can be determined only by experimentation. Neither can one tell by looking at seeds whether they are pure dominants, hybrids, or pure recessives for most characters.

Mendel's studies were reported to a small society of naturalists and published in the obscure transactions of that society in 1866. Here they

lay buried until 1900 when Hugo de Vries and two other European biologists independently discovered them.

In recent years Mendel's experiments have been extensively repeated on plants and animals of many kinds. They have been abundantly confirmed and considerably amplified. It has been found that allelomorphic pairs do not always stand in the relation of dominant and recessive, for in some cases a character may appear intermediate between those of the two parents. For example, crosses between red and white snapdragons have yielded all pink flowers in the F_1 generation and in the F_2 generation one-fourth red, one-half pink, and one-fourth white flowers. We have here an example of *incomplete* or *imperfect* dominance.

We pay tribute to an obscure monk for discovering two of the most vital principles on which the science of genetics is founded, namely, (1) that any given heritable character of the parent may appear in the offspring independently of other characters, and (2) that contrasting pairs of characters usually reappear in certain generations of the offspring in a numerically definite proportion.

Chromatin Behavior in Hybrids

While Mendel's work was going on and being verified and amplified, and through all the years since his time, equally brilliant researches have been conducted under vastly greater difficulties in an effort to find a *physical basis* for heredity. Successively the following facts were brought to light: (1) Living things are composed of cells. (2) In sexual reproduction each parent contributes a germ cell. (3) Through the nucleus hereditary tendencies are transmitted from parent to offspring. (4) Each nucleus has a definite number of chromosomes. (5) Chromosomes have an individuality that is maintained indefinitely. (6) In the final steps of conjugation there is an intimate association of individual male and female chromosomes. (7) In the conjugation of chromosomes they pair in a definite way. Each male chromosome pairs with a *homologous,* or corresponding, female chromosome and no other. (8) Each chromosome contains units called *genes* which, singly or in unit groups, are responsible for the transmission of specific tendencies. (9) The genes in a zygote are in homologous pairs, one in a male chromosome and one in a corresponding female chromosome. If both homologous genes in a zygote carry the *same* hereditary tendency, as tallness, the resulting plant is *homozygous* for tallness. It is a pure strain for tallness and will breed true if self-pollinated. If the two homologous genes

in a zygote carry *opposite* tendencies, as one tending toward shortness and the other toward tallness, the resulting plant is ***heterozygous*** for tallness and shortness. It will not breed true but will yield some short and some tall offspring.

Chromosome Reduction.—When the nuclei of gametes unite, the chromosomes remain distinct for a time. We have, then, in the life history of the plant a period in which the chromosome number is 2n. The time for the reduction of the chromosome number to n varies in different groups of plants, but in the Bryophytes, Pteridophytes, and Spermatophytes, and in some of the Thallophytes it is reduced in the two nuclear divisions that take place when a spore mother cell divides to form four spores. This process of nuclear division that results in chromosome reduction is called *meiosis*.

In the first nuclear division of the spore mother cell the spireme thread is double, i.e., composed of two strands, one consisting of the male chromatin and the other of the female chromatin carried through the plant from the zygote. In this spireme thread the chromosomes are arranged end to end, and the homologous male and female chromosomes lie side by side in close contact. *Chromosome conjugation* now takes place. In this process the male and female parts of the spireme thread press tightly together and twist about each other to some extent. The union is so complete that the spireme looks, for a short time, like a single strand, and apparently some exchange of material takes place between the homologous chromosomes, which have not lost their identity. After conjugation this spireme breaks by transverse division into paired chromosomes which may still be called male and female although, as a result of conjugation, each has taken some of the properties of the other. Now, or perhaps earlier, each male and each female chromosome splits lengthwise. As a result there are four homologous chromosomes, called *chromatids,* in bundle-like groups. Two are male, resulting from a splitting of the male chromosome, and two are female, resulting from a similar splitting of the female chromosome. All this takes place in the early stages of nuclear division in a spore mother cell whose nucleus goes to make up the four nuclei of the four spores. Each chromosome that was formed by the conjugation of a male with a female has been divided into four chromatids, and in the first and second reduction divisions that now take place the chromatids separate and one goes to each spore nucleus, where it becomes a chromosome.

It is a matter of great importance in relation to Mendel's law that any one of the four chromatids of a chromosome may happen to go to

any one of the four spores, and any spore may happen to get one chromatid of one chromosome and a different chromatid of another chromosome. It is also significant that in the process of chromosome conjugation each chromosome has taken up some of the properties of its mate of the opposite sex, and the two have thus become more or less alike but still remain somewhat different. Apparently variation, which is so vital to evolution, is determined in part at least by the exchange of materials in chromosome conjugation and by the combination of chromatids that goes to any spore.

Suppose, for example, in the spore mother cell we call the male chromatin M and the female chromatin F. When chromosome conjugation takes place the spireme will be MF. When the spiremes separate again and then each splits, we can call the four homologous parts M, M^1, F, F^1. The pea has seven chromosomes (haploid), and each spore will get a representative part of each of the seven chromosomes, 1, 2, 3, and so on, but it may be part M, M^1, F, or F^1 from chromosome 1, and the same or any other part from any other chromosome.

Distribution of Genes and Mendel's Law.—In the example given above let us suppose that the *factor* (gene or group of genes) for tallness and its contrasting allelomorph, the factor for dwarfness, are in chromosome number 1. The pollen was taken from a pure-line tall plant and placed on the stigma of a pure-line dwarf plant. The M (male) chromosomes would then bear the dominant factor for tallness and the F (female) chromosomes would bear the recessive factor for dwarfness.[1] These factors both enter the zygote nucleus in the ovule but remain separate for a time, in fact throughout the vegetative growth of the pea plant until the flowers appear. The result is an embryo sporophyte growing to maturity with 2n chromosomes, and since tallness, the M factor, is dominant, the seeds all produce tall plants. In their flowers reduction of chromosomes takes place in the divisions of the spore mother cells to form the microspores and megaspores. In this process male and female chromosomes number 1, containing the factors for tallness and shortness respectively, conjugate, then split, thus forming parts M, M^1, F, and F^1 of chromosome number 1. Thus in an anther of this hybrid plant a given pollen grain may get either one of the two males, M or M^1, or either one of the two females, F or F^1. Likewise, in an ovule of

[1] It should be understood that if pollen had been taken from a pure-line dwarf plant and placed on the stigma of a pure-line tall plant the resulting offspring would have been the same, but in that case the F chromosomes would have carried the dominant factor for tallness and the M chromosomes the recessive factor for dwarfness.

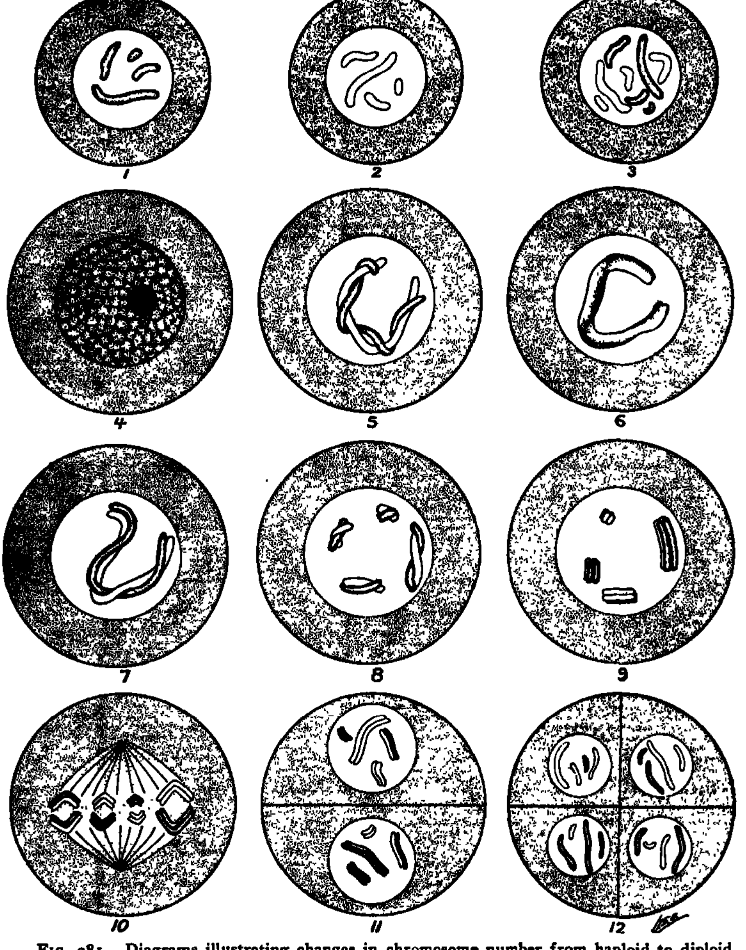


FIG. 281. Diagrams illustrating changes in chromosome number from haploid to diploid, followed by reduction from diploid to haploid. The male chromatin is shaded, and the female chromatin is left white. 1, male gamete (haploid); 2, female gamete (haploid); 3, zygote and cells of the sporophyte generation (diploid); 4, spore mother cell in the resting condition (diploid); 5, male and female spireme threads ready to conjugate (diploid); 6, male and female chromosomes conjugating (diploid); 7, separation of spireme threads after conjugating (diploid); 8, paired chromosomes that have originated from the cross division of the spireme threads (diploid); 9, chromatids in groups of four resulting from a longitudinal division of the chromosomes (transitional); 10, spindle fibers drawing spermatids to the poles (transitional). Note that two male chromatids, or two female, or one male and one female, may go to either pole. 11, two cells formed from the first reduction division of the spore mother cell (transitional); 12, four spores, each containing in its nucleus one spermatid from each set. These have now become the chromosomes of the spore nuclei (haploid). Each spore grows into a gametophyte which produces a gamete—either male or female.

the same plant a given megaspore may get either a male, M or M^1, or a female, F or F^1. The tiny gametophytes and the gametes that come from these spores have nuclei with the same factors as the spores and the same combinations of chromosomes.

We can now account for the distribution of tall and short plants in the second filial generation and thereafter in accord with Mendel's law:

(1) If a male gamete having chromosome M or M^1 unites with an egg having chromosome M or M^1, the resulting plant will be tall and a pure-line dominant for tallness.

(2) If a male gamete having chromosome F or F^1 unites with an egg having chromosome F or F^1, the resulting plant will be short and a pure-line recessive for shortness.

(3) If a male gamete having chromosome M or M^1 unites with an egg having chromosome F or F^1 (or vice versa) the result will be a tall plant, but heterozygous for tallness and shortness, and its offspring may be tall or short, depending on the chromosome combination that takes place in the next generation. By the law of chance we would expect one-fourth of the plants in this generation to be pure, or homozygous, dominants, one-fourth pure, or homozygous, recessive, and one-half heterozygous, or hybrids.

It is a splendid tribute to the work of Mendel and the work of the cytologists, carried on independently until the last few years, that their findings, arrived at by wholly different methods, should coincide so perfectly.

The Products of Evolution

By processes that follow natural laws a vast assemblage of plant species has been formed. Some 240,000 of them still survive. To trace all of these, or indeed any of them, with certainty back to the original ancestor would be a remarkable achievement. Doubtless it would carry us through some species that are now quite extinct. The individual ancestors are long since gone. The ancestral species are likewise gone. We have reason to suppose that some of the existing species of lower plants are more like the ancestral species than are any of the higher plants. In other words, some species have progressed less than others. Also some lines have progressed in one direction and some in another, but many primitive characters have been retained.

In recent years a number of botanists and zoologists have attempted to piece together the fragmentary evidence that has been accumulated into a connected account of the progress of evolution. Diagrams in the

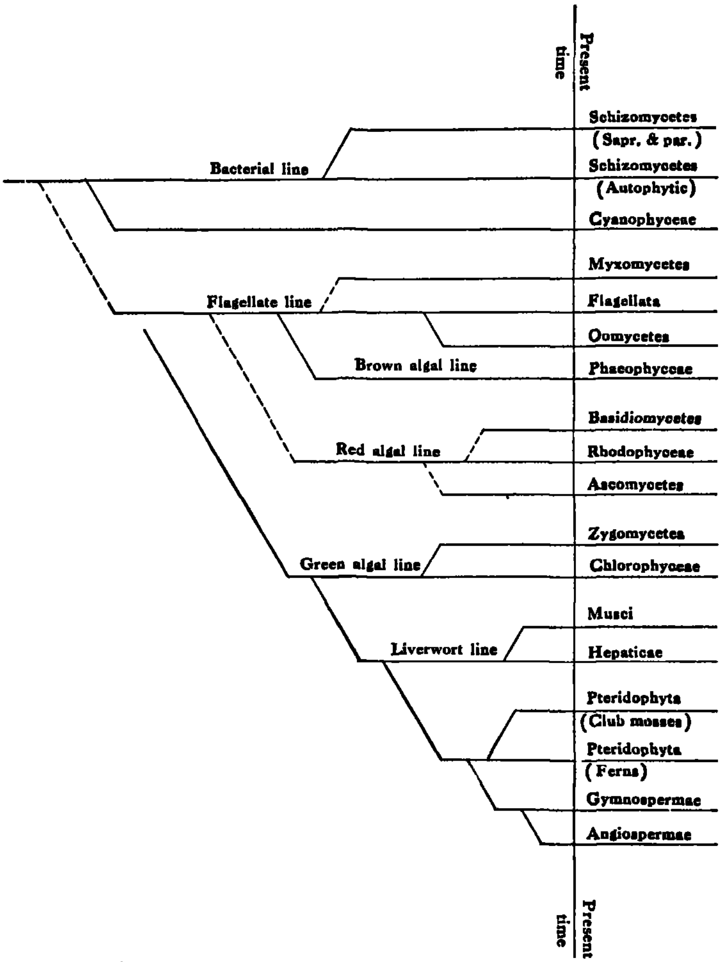


FIG. 282. Diagram suggestive of the relationships that may exist between groups of plants, past and present.

form of trees are sometimes used for this purpose. The best of these probably are accurate in some portions, but in others they are only speculative and suggestive. Nevertheless they have a value as a basis for discussion, and for this purpose only, a tentative scheme of classification of the plant kingdom given in Figure 282 is placed before the student.

Review Questions

1. What is the prevailing scientific opinion as to the time and place of the origin of life on the earth?
2. What is your conception of the structure of the first living things?
3. How did they probably obtain energy for their needs?
4. What two great principles underlie Darwin's conception of the origin of species?
5. Which may be regarded as the dynamic principle and which as the guiding principle in evolution?
6. Are all variations in the direction of higher development? Explain.
7. Are variations in the nature of benefit or harm to the race, or is there no rule?
8. State St. Hilaire's explanation of variation.
9. Why is this not an explanation of evolution?
10. State Lamarck's explanation of variation.
11. What is the weakness of Lamarck's explanation?
12. What three facts did Darwin use as a basis for his theory of origin of species by natural selection?
13. How did Darwin and de Vries differ in their explanation of evolution?
14. From the standpoint of chromatin behavior, how can variation be explained?
15. What is meant by orthogenesis?
16. How does it help to explain evolution?
17. Who did the first *exact* experimentation in heredity?
18. In what sense did Mendel use the expressions "dominant" and "recessive"?
19. To what extent would it be possible to predict in advance which of a pair of contrasting characters will be found dominant?
20. What is meant by a pair of allelomorphs?
21. If tall (dominant) peas are crossed with dwarf (recessive) peas and allowed to self pollinate after the F_1 generation, what will be the proportion of tall and short plants in the F_2 generation?
22. If the total number of tall and short plants in the F_2 generation is 32, how many will be pure-line tall and how many pure line dwarf, and how many hybrid, i.e. not pure line?
23. Define (1) gene, (2) hereditary factor, (3) allelomorph, (4) monohybrid, (5) dihybrid, (6) meiosis.
24. What two important principles were illustrated by Mendel's experiments?

25. Explain what is meant by homologous chromosomes.
26. At what stage in the life history of an Angiosperm does the chromosome number change from haploid to diploid?
27. At what stage does the number reduce to haploid?
28. In the first division of the spore mother cell, what is the character of the spireme thread?
29. What takes place in chromosome conjugation?
30. After the spiremes have conjugated and separated, and each has split, how many homologs are there of each chromosome?
31. What cells will finally receive each of these?
32. What determines which of the homologous chromosomes will go to a given spore?
33. How could variation be accounted for on the basis of chromosome conjugation?
34. If smoothness of seeds is a dominant character and roughness of seeds is a recessive character, and if in the third hybrid generation there are 64 seeds, how many would be smooth and how many rough?
35. If in the case just given this character is determined by a factor in chromosome number 1, and if in a given cross the dominant allelomorph is in the female gamete and the recessive in the male gamete, what chromosome combination in the zygote would result in: (1) a pure-line smooth-seeded variety? (2) a rough-seeded variety? (3) a hybrid variety that will yield some smooth seeds and some rough seeds?
36. Give an example in which the offspring is intermediate in a given quality between the two parents.

CHAPTER XXVI

FOSSIL PLANTS AND THEIR SIGNIFICANCE

For hundreds of years fossil remains of plants and animals have been found accidentally and more recently have been sought for most zealously. When fossils were first discovered their significance was not comprehended, and strange, weird, and even superstitious explanations were offered to account for their presence. Not until a little over a century ago was it generally conceded that these interesting objects are the stony remains or the imprints of once living individuals. When this fact is coupled with the knowledge obtained by geologists that different strata of the earth's crust were laid down at different periods of time, we have a strong line of evidence bearing on the evolutionary origin of the plants and animals we see about us. The evidence obtained from fossils greatly impressed Darwin in his researches on evolution.

Decay and Fossilization

When plants and animals die they usually decay rapidly and disappear, but sometimes they become fossilized instead. Why the difference? Briefly, if conditions are suitable they will decay, and that rather promptly, except for a few resistant parts such as the bones and teeth of vertebrates and the shells of mollusks. If conditions are not suitable for rapid decay the bodies may slowly change into fossils.

Conditions Favoring Decay.—Decay is the result of the physiological activity of many species of fungi and bacteria. With their digestive enzymes they dissolve the tissues of dead bodies and use them for food. Stumps and logs in the forest may resist this devastation for years, but ultimately they succumb. The same conditions that favor the development of these organisms will also favor decay. Conversely, where these organisms cannot thrive decay will not take place.

Such organisms as *Bacillus subtilis, Penicillium,* and a host of others that take part in decomposition are found practically everywhere, associated with plants and animals. They have little effect on living things but readily attack their bodies after death. There are four chief

requirements for their development: (1) suitable food, (2) moisture, (3) oxygen supply, and (4) favorable temperature. Where plant and animal bodies, and fallen leaves and other plant parts come to rest, these four conditions together with the necessary organisms usually exist. Hence, most plant and animal refuse decays, becomes incorporated into the soil, and is lost beyond further recognition. Probably not one plant in a million ever became fossilized, and in some groups perhaps none of them ever did.

Conditions Favoring Fossilization.—The conditions under which *fossils are produced are exceptional.* Most fossils are the remains of plants and animals which were covered deeply with mud. Volcanic mud, lake mud, ocean sediments, and the silt from overflowing rivers have all played their part. Under these conditions the factor inhibiting decay is usually lack of air.

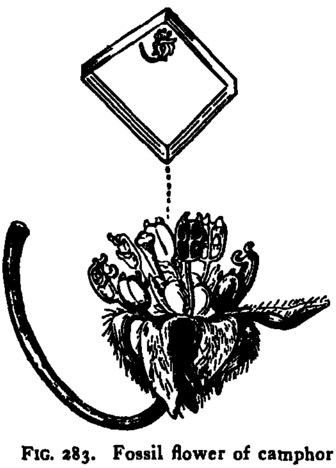


FIG. 283. Fossil flower of camphor tree, preserved in amber. Upper figure natural size; lower figure enlarged. (From Knowlton's *Plants of the Past,* Princeton University Press. After Göppert and Menge.)

It should not be inferred that *decay and fossilization* are wholly distinct, for quite commonly the processes of decay go on slowly at the same *time* that the fossils are being formed in ways that will now be described.

Methods of Fossilization.—Most fossils are preserved in sedimentary rocks of sandstone or limestone, or in coal or shale. To be preserved the specimen needs to be buried alive, or soon after death, in material that will harden about it. There are two classes of fossils, those that form by simple *inclusion* and those that form by *infiltration.*

Fossils that have formed by inclusion are by far the most common. The plant or part is suddenly buried in a soft material that hardens gradually under pressure. If this material is very fine it preserves with wonderful detail the shape of the plant or animal and all the surface markings. The most perfect imbedding material is amber, which is a fossilized resin. Meanwhile the specimen itself is undergoing change. Gradual decay may destroy it entirely, leaving a *mold.* This may remain

empty or it may be slowly filled with mineral matter—calcium carbonate, for example—forming a *cast*. In other cases a part of the organic material will remain, reduced to a coal-like substance in which the structure may or may not be partly preserved. By the method of inclusion soft-bodied algae, fungi, bacteria, and flower petals have been recorded in the rocks, as well as worms, jellyfishes, and even tracks of animals and prints of rain drops in the mud.

FIG. 284. Fossil leaves preserved in rock. (From Knowlton's *Plants of the Past*, Princeton University Press.)

The less common method, but one that makes superior specimens for study, is by infiltration after inclusion. This process is at its best in the preservation of wood and other hard plant materials. A whole growing forest may be buried in volcanic ash or mud, after which infiltration sets in. Chemicals, usually silica, lime, or magnesia, dissolved in the water penetrating the sediment in which the plant is embedded gradually replace the water of the plant tissues and the organic matter also. The wood is thus petrified. This infiltration preserves not only the surface markings but the cellular details within. Sometimes even the fungi and bacteria that have penetrated the wood and caused partial decay are visible in sections of such fossils.

FIG. 285. Three views of a piece of petrified wood of elm, about one-third natural size

What We Learn from Fossils

The search for remains of once living plants and animals is most fascinating. In natural burial grounds millions of years old, in tombs of solid rock, lie bodies of every description. Some represent species long since extinct, wholly unlike any living thing. Others are survived to the present time by their own descendants, either the same species or more highly developed ones derived from them.

Most fossils are discovered by breaking open rocks, and part of the fascination of the search lies in the constant uncertainty as to what a blow of the hammer may reveal. The experienced paleontologist has an advantage over the novice, but this advantage is sometimes rudely overturned by the element of chance. A few of the finest specimens known have been uncovered by amateurs who saw for the first time the remains of plants and animals that were buried long before primitive man faced the problems of life. Unfortunately certain kinds of fossils are extremely fragile, and many have been ruined by well-meaning but inexperienced collectors.

The record of the fossils is like a huge puzzle map, the pieces of which have been scattered far and wide and many of them destroyed. A single fragment has little meaning in itself, but fitted into its place with others it helps to make a great picture. It is unlikely that all parts of the puzzle will ever be recovered. Some very significant plants and animals may never have been preserved in the rocks. Some have been destroyed by the same forces of erosion that have worn away mountains. Some have become obliterated by the commercial processes of man—mining, road building, agriculture, etc. Many have also been discovered during these same operations. Some may be close at hand but safely hidden. Some are buried in the ocean bed where they will lie for ages until a slow upheaval raises them together with the rocks in which they rest.

Notwithstanding these inevitable difficulties, man's determination has been richly rewarded during the past century. The story is still fragmentary, and we are prone to fill in the gaps by imagination, but a much fuller and more authentic account of prehistoric life than most people realize is now available.

Application of Paleontology.—The scientific value of the findings of paleontology extends into several fields.

(1) The subject is closely related to historical geology. Whatever theory is accepted as to the origin of the earth, all are agreed that its

surface layers have been folded, broken, elevated into mountain ranges, and eroded. In the regions where the rocks are stratified, the deeper strata were deposited first and the surface strata last. Where this stratification has been little disturbed it is easily followed by the geologist, but in places it has become so irregular that the identification of the layers could hardly be made were it not for the fossils they contain.

(2) Each portion of the earth's crust was deposited during a certain span of time. Plants and animals have continually adapted their structures to environmental conditions, especially temperature, moisture, and food supply, and so the climates of past ages are recorded with unerring fidelity by fossil plants and animals. The finding of ancient corals and of bread fruit and other tropical plants in Greenland and adjacent North America shows that this ice-bound area once had a tropical climate. Fishes, mollusks, and turtles live in water and their presence in the rocks of high mountains and plains, as in Wyoming and Montana, shows that these regions, though they may now be semi-arid, were once sea bottom; and the finding of plants and animals typical of marsh lands in other strata of the same regions shows a transitional stage between the submerged condition and the desert.

(3) The course of evolution in both the plant and animal kingdoms can be traced with considerable accuracy by the fossils, except for numerous gaps that are being gradually filled in. The oldest fossils are of very primitive forms of life. Among them are found no vertebrate animals or seed plants or even mollusks or ferns. These higher forms of life could hardly have existed when the earliest fossils were formed, for, with their bones, shells, or hard woody tissues, they would have been preserved much more readily than the algae and soft-bodied primitive animals. Higher up in the earth's crust are strata characterized by ferns, lycopods, and fishes, but destitute of flowering plants, birds, and mammals. In the youngest rocks are found plants and animals of all kinds, both higher and lower.

The Geological Time Table.—For convenience in portraying the fossil record of the rocks of different ages, diagrams have been made of a section of the earth's crust as it would be if undisturbed by folds, faults, erosion, etc. From these diagrams and other available information the following table has been prepared. This is based on a calculation that geologic time is about 1,500,000,000 years, and that the first primitive life on the earth appeared perhaps 1,000,000,000 years ago.

In the geologic time table given on page 403, only the upper half of the paleontological record is shown. Older than the Paleozoic era is

the Proterozoic era in which some remains of simple life are found, and still older is the Archeozoic era where recognizable fossils are extremely rare, but where deposits of calcium carbonate and of graphite testify that living things existed in considerable abundance.

GEOLOGIC TIME TABLE

UPPER HALF OF PALEONTOLOGICAL RECORD

Era	Period	Climate and forms of life
Cenozoic era: dominance of angiosperms and mammals	Late Cenozoic 25,000,000 yrs. ago	Ice caps and glacial conditions extending from poles into temperate zones. Extinction of many large mammals and trees. Dominance of herbaceous plants. Beginnings of civilization. Elevation of the Swiss alps and the Andes.
	Early Cenozoic 60,000,000 yrs. ago	Climate fluctuating, mostly warm and humid. Extension of forests, increase of birds and mammals, appearance of primates. Elevation of the Pyrenees.
Mesozoic era: dominance of gymnosperms and reptiles	Cretaceous 120,000,000 yrs. ago	Climate tropical, then cooling. Elevation of Rockies. Coal deposits from gymnosperms.
	Jurassic Triassic 170,000,000 yrs. ago	Temperature moderate but rising. Lands extending. First angiosperms and mammals.
Paleozoic era: dominance of pteridophytes and fishes	Permian 210,000,000 yrs. ago	Climate dry and cold. Gymnosperms waning, land vertebrates increasing.
	Carboniferous 285,000,000 yrs. ago	Climate at first cool, finally becoming glacial. Extensive coal deposits from pteridophytes and gymnosperms.
	Devonian Silurian Ordovician 410,000,000 yrs. ago	Climate warm, arid in central regions. First gymnosperms, fishes, and amphibians.
	Cambrian 500,000,000 yrs. ago	Temperature warm over entire earth. First pteridophytes and trilobites.

Succession of Plants and Animals Through the Ages.—When we bring together all the evidence that has been unearthed by paleontologists and interpreted by men from different branches of science, we obtain an account of evolution that is most illuminating.

Life seems to have begun on the earth in the Archeozoic era in a very simple form that could live independently but had not yet evolved

the mechanism for utilizing the light of the sun as a source of energy for food manufacture. From it may have come the autotrophic bacteria, the blue-green algae, and low forms of animal life, all of which left their records through the Proterozoic era. By the beginning of the Paleozoic era—the Cambrian period—blue-green algae, bacteria, and sponges were abundant, and probably some other algae, trilobites, worms, and gastropods.

During the Paleozoic era the diversification of life was tremendous. This development was partly in the ocean but also on the land. From the simple beginnings just mentioned plants advanced in the sea to a great wealth of all classes of algae. Liverworts [1] appeared on the land and then Pteridophytes, which reached their climax in the middle of the Carboniferous period and were superseded late in that period by the Gymnosperms. During this era fishes appeared, then amphibians and reptiles along with insects and other arthropods.

The Mesozoic era saw the origin and rapid increase of Angiosperm forests and the decline of Gymnosperms. Great dinosaurs appeared, flourished for a time, and became extinct. Toothed birds and flying reptiles had their period of prosperity. Some of the smaller reptiles gave origin to primitive mammals the size of rats.

The Cenozoic era has brought about less change in plants than in animals. There has been waning of forests, partly from the rigors of the glacial epoch and partly from the ravages of man. Grasses and other herbaceous plants have evolved and taken their place. Archaic mammals have disappeared and have been replaced by a multitude of modern mammals and primates, including man.

Thus is recorded in the rocks the eloquent story of how life, through endless variation and the relentless change of environment, has covered the earth with highly specialized beings and a residue of the unprogressive things that survived but could not evolve higher.

Review Questions

1. What determines whether a plant after death will decay or fossilize?
2. Describe two methods by which fossils are formed.

[1] The statement that liverworts appeared before Pteridophytes is based on the comparative morphology of the two groups. Fossil Pteridophytes have been found in older rocks than have fossil liverworts, but it may be that the earlier liverworts left no fossils, or that no one has been so fortunate as to find them. There is a difference of opinion as to the relative antiquity of the two groups.

3. Which of these methods best preserves the internal structure?
4. By which of these methods is wood petrified?
5. In what way do fossils aid the geologist?
6. How may fossils indicate the character of a prehistoric climate?
7. How do fossils support the doctrine of origin of species by evolution?
8. If you wanted to place a fern leaf under conditions that would cause it to form a fossil, how would you do it?
9. Explain how the presence of limestone or graphite indicates the existence of life there in ages past.
10. Name some gaps in the evolutionary history of plants that need fossils not yet found to bridge them over.

Part Eight

RELATION OF PLANTS TO EACH OTHER AND TO ANIMALS

CHAPTER XXVII

PLANTS THAT ARE NOT INDEPENDENT

Thus far we have, for the most part, considered plants that lead a relatively independent life. There are many indirect ways in which plants affect each other's welfare, and these will be considered presently. Some plants possess chlorophyll, utilize the sunlight, and manufacture their own food. Such plants we call *autophytes*. On the other hand, *saprophytes* are dependent for their food on a supply of non-living organic matter, while *parasites* attack living things of other species and obtain their food from them.

Origin of Saprophytism.—It is generally agreed that saprophytes evolved from autophytes. Not merely a single group of green plants but several among the algae and the flowering plants appear to have yielded saprophytic progeny. Positive proof of the method by which saprophytes originated cannot be given at this time, but it was probably in harmony with known laws of evolution.

The transition to a saprophytic habit involves several readjustments: (1) loss of chlorophyll, (2) increase in absorptive organs, (3) increase in digestive powers, and (4) increase in reproductive powers. During the course of evolution, variation appears to have taken place repeatedly in every conceivable direction. If variations in the direction of saprophytism took place in plants closely associated with organic refuse, the plants would receive great benefit from the rich supply of available food and would be better fitted to survive than were their ancestors, even though they lost the chlorophyll which they no longer needed and which is expensive to make. If, on the other hand, the change to saprophytism took place in an environment where organic food was scarce, it would have a negative survival value, as the plants would be less well fitted to survive than their autophytic ancestors. There can be no doubt that many saprophytes do starve at the present time, when they are so unfortunate as to become stranded in an inorganic environment, and it is conceivable that during the progress of evolution many saprophytic lines became extinct.

The great groups of saprophytes are the bacteria and the fungi, and

their powers of digestion, absorption, and reproduction have already been referred to. Among the flowering plants two small groups, the Monotropaceae, commonly known as Indian pipe, pine-drops, or pine-

FIG. 286. Left, Indian pipe, *Monotropa uniflora;* right, Pine-sap, *Hypopitys lanuginosa;*—two saprophytic flowering plants. (From Dixon's *The Human Side of Plants.* Frederick A. Stokes Co.)

sap, and the genus *Corallorhiza* of the orchid family, are well known in the United States, while some others are found in the tropics. These plants are characterized by absence of chlorophyll, small scale-like leaves, extensive systems of fine roots, and many very tiny seeds. Evidently the saprophytic habit is not well suited to the development of flowering plants, for the number of species and individuals is few as compared with

their green relatives on the one hand and the saprophytic fungi on the other.

Origin of Parasitism.—The origin of parasitism has been somewhat more varied than that of saprophytism. Some parasites have come from saprophytes and others from green plants. It is notable, too, that while parasites are proportionately fewer than saprophytes among the bacteria, and especially among the fungi, they are somewhat commoner among the flowering plants, examples being known in at least four families.

The evolution of parasitism is much easier to trace than that of saprophytism because of the existence of intermediate forms—connecting links as it were. First let us consider the transition from saprophytism to parasitism, which is the usual change among the fungi. *Rhizopus* and *Penicillium,* for example, are commonly classed as saprophytes. They cannot attack young vigorous plants; but ripe fruits, and fleshy roots such as carrots, with cells still alive, readily fall a prey to them. They are *facultative* parasites. Going a step further, there are known among the Ascomycetes hundreds of species that regularly cause plant diseases and are classed as parasitic fungi. However, the majority of these grow well in artificial culture media in the laboratory, passing through the entire life cycle there. They have retained some of their ancestral saprophytism. Lastly, there are the strict parasites—the powdery mildews and the rusts—that require a living host for their development.

The change from autophytes to parasites is the one usually occurring in the flowering plants. Complete parasitism is not usually attained here, for the leaves of the parasite remain green (though often pale) and are partially functional. Parasitism in this class has taken three different forms. (1) In the Orobanchaceae, the Santalaceae, and some of the Orchidaceae, the seeds of the parasite germinate in the soil and the plants start in the normal way. Unless their roots find those of a suitable neighboring plant the potential parasites do not thrive and generally fail to reach maturity. If they do find such roots they send haustoria into them and grow vigorously. Some of them are so normal in appearance that their connection with a host root would not be suspected. Others have small scale-like leaves with little chlorophyll and are almost wholly parasitic. (2) In the dodders, of the family Cuscutaceae, the seed of the parasite germinates in the soil and a slender stem rises into the air. If this succeeds in finding a suitable host it twines about it and sends haustoria into the stem. The stem of the parasite below the point of

FIG. 287. Alfalfa dodder, *Cuscuta planiflora*, twining about alfalfa plant and attached by haustoria.

attachment fails to develop further and dies. Thereafter the dodder is dependent upon its host and the limited activity of its small, pale green leaves and stems. (3) The parasitism of the mistletoes, belonging to the family Loranthaceae, starts somewhat differently. The seeds are viscid and are carried about accidentally by birds, squirrels, etc. If they fall to the ground they die, but if they reach the bark of a suitable

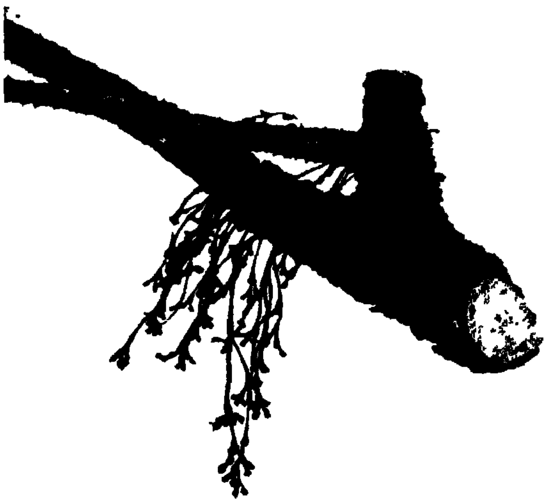


FIG. 288. Lesser mistletoe, *Arceuthobium Americanum*, growing on lodgepole pine.

host they germinate and attack it by means of haustoria. The leaves are pale green and the parasitism is not complete.

It may here be noted that the largest known flower is produced by a parasitic plant, *Rafflesia Arnoldii*. It grows in Sumatra and is parasitic on the roots of certain tropical vines. The flower of this plant is approximately one meter in diameter.

Significance of Saprophytism and Parasitism.—We have been trained to admire independence. We hold in some contempt any form of life that is noticeably dependent. Hence we call saprophytism, and especially parasitism, *degeneracy*. But is it? In one sense yes, for the organism has lost some useful thing, usually chlorophyll, that its ancestors possessed. On the other hand some saprophytes and parasites have

gained more than they have lost. They have progressed in that they have evolved new methods of obtaining food. The fungi get on quite as well as the independent algae, *so long as their habitat includes suitable organic food.* Should this disappear their fate would be that of other plants and animals that have depended too much on specialization in one direction. Even as matters stand today saprophytism and para-

FIG. 289. Giant flower of *Rafflesia Patma* growing parasitically on the roots of a vine. (From Kerner's *Natural History of Plants*, Blackie & Son.)

sitism have been more of a handicap than a benefit among the few Angiosperms that have adopted them.

It should be further remarked that in no instance has a saprophyte or a parasite evolved into anything much superior to itself. That which benefits the individual has been a stumbling block to the advancement of the race. What might be classed as a moral issue among men is a stern reality among plants and the lower animals.

Interdependence of Species.—Aside from the extreme dependency of saprophytes on the products of other forms of life, there are less obvious ways in which one plant profits by the existence of another. It is scarcely too much to say that no one species could survive alone. While the green plants can make their own organic food by photosynthesis, they and all the other plants have other nutritional difficulties. What keeps up the supply of suitable nitrogenous food, chiefly nitrates, in the

soil? What maintains the oxygen supply of the air? These questions are best answered by a sketch of the changes brought about by the activities of different forms of life. (1) Green plants, when exposed to light, constantly take up carbon dioxide from the air and release oxygen. (2) Animals, and saprophytic and parasitic plants, derive much of their food and chemical energy directly or indirectly from these green plants. (3) All living things release carbon dioxide into the air in exchange for oxygen. (4) Bacteria and fungi break down the protoplasm and other proteins of dead plant and animal bodies and use it for their own purposes, but ultimately they leave it in the form of nitrates, the most usable form of nitrogen for most green plants. (5) In the processes of decay brought about by certain bacteria there is an escape of free nitrogen into the air. This in itself would ultimately result in nitrogen starvation for all plants and animals but for the nitrogen-fixing bacteria that bring the free nitrogen of the air back into combination with other elements.

Thus it may be seen that there now exists a highly complex interdependence of species far outweighing in mutual benefit the harm done by those species that have become parasitic.

Review Questions

1. What name is applied to: (1) plants that are relatively independent through ability to manufacture their own food? (2) plants that obtain their organic food from non-living organic matter? (3) plants that take their organic food from living things?
2. Give an example from each of the groups in question 1: (1) from the lower plants, (2) from the higher plants.
3. What morphological or cytological modifications usually accompany the change: (1) from autophytes to saprophytes? (2) from autophytes to parasites?
4. What is the distinction between strict parasites and facultative parasites? Give an example of each.
5. Explain why most saprophytes and parasites need no chlorophyll and how their evolution from autophytes may have come about.
6. Under what conditions would the adaptation to a parasitic habit of life be a detriment to a plant?

CHAPTER XXVIII

COMPETITION AMONG PLANTS

There is no evidence of a deliberate mutual helpfulness in plants either among species or among individuals. Each responds to its own inherited tendencies and to its environment. Each plays a part in creating an environment for its neighbors, and this environment may be either beneficial or harmful. There may be a limited supply of certain necessities, particularly food, water, and light, and, if so, one plant may get its supply at the expense of another. While competition often involves two or more of these factors acting together, the influence of each one will have to be considered separately to avoid confusion.

Competition for Food.—The most intense competition for food occurs among saprophytic bacteria and fungi. If the supply of organic matter is small, those that can absorb it rapidly have a tremendous advantage. If the supply is large, the competition takes the form of a race in development and reproduction. A fertile soil may contain more than 10,000,000 bacteria per gram and be interwoven with the mycelium of fungi. Under these crowded conditions there is an actual *antagonism*, a chemical warfare between species which destroys vast numbers of the competing individuals. As a rule bacteria will outdo fungi in an intense competition, but there are many exceptions, and much depends on the species involved and on the kind of food available. Where several species are competing, as is usually the case, the only chance for a slow-growing one is that it may be able to use something of a kind that was rejected by the more vigorous ones.

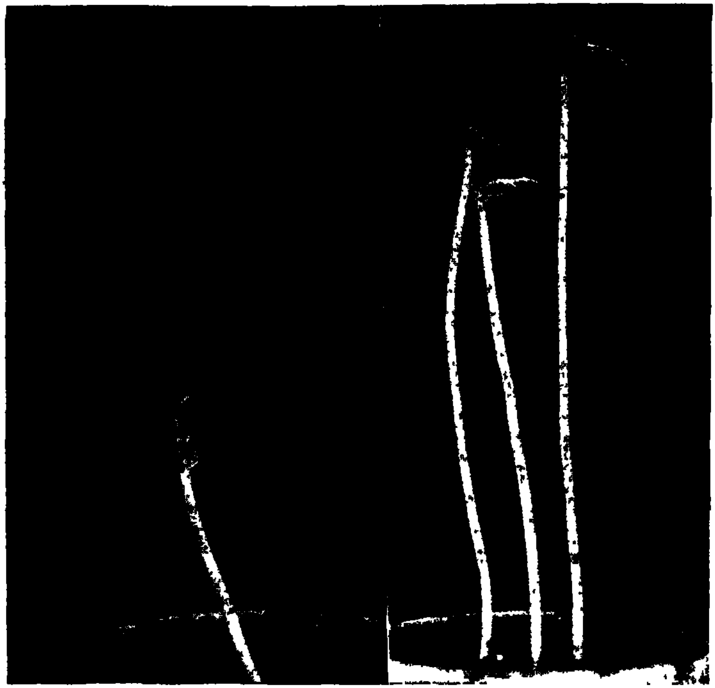
Competition for food materials among the higher plants is usually not so intense as that for moisture or light.

Competition for Space.—Space for growth is apparently a limiting factor in plant development, and we often say that plants are too crowded to grow well. It is rare, however, that actual contact with neighboring plants is the most important factor in crowding. More often the trouble is due to a scarcity of light.

Competition for Moisture.—This form of competition is more in evidence among flowering plants than among lower plants, largely be-

FIG. 290. Plant association. In the background is *Pinus heterophylla*. As an undergrowth is a small palm—*Sabal serrulata*. Covering the ground between is grass of various kinds. (From Schimper's *Plant Geography*, The Clarendon Press, Oxford. After Webber.)

cause of their greater size and demand. There are two conditions in the growing of economic plants in which this competition for water is strongly in evidence. Crops often grow poorly near trees and hedges. These larger plants are said to "sap the soil." This may be due in



A B

FIG. 291. A, normal bean seedling, grown in strong light, contrasted with B, bean seedlings of the same age grown in darkness and etiolated.

part to competition for food and for light, but often it is most conspicuous on the sunny side of a hedge or tree in a rich soil with an insufficient rainfall. A second example is in the competition between vigorous weeds and growing crops. Moisture is lost from the soil by direct evaporation and by the transpiration of plants growing on it. It may be argued that if weeds shade the soil they will thus reduce evaporation, but experiments have shown that the transpiration of a growing crop removes much more water from the soil than does the

sun shining directly upon it. Often the roots of the weeds have about the same feeding depth as those of the crops with which they are competing and thus make serious inroads into the water supply.

Competition for Light.—Light is the life of a green plant. When plants are not crowded, each branches and spreads its leaves to the sun-

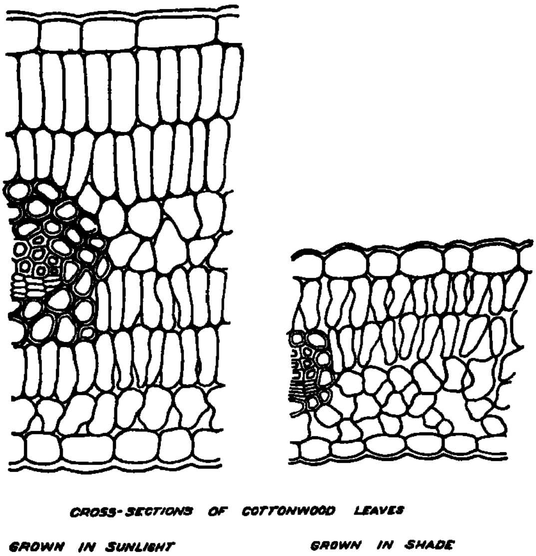


FIG. 292. Effects of light on leaves of cottonwood. With insufficient light the palisade cells and the mechanical tissues of the veins are poorly developed. (From laboratory form by Transeau, Ohio State University.)

light in whatever way best suits its needs. Often, however, many plants of the same and different species are competing intensely for positions between the others and the sun. Here trees have an advantage over smaller plants so that in a very dense forest the light may be too weak for any undergrowth to succeed. The more rapid elongation of plants in the darkness or shade than in the direct sunlight makes crowded plants taller than isolated ones. Branches fail to develop on the lower part of the plant if light there is too weak. Often they make a limited growth and then die. Furthermore, the mechanical tissue in the xylem of a shaded plant is poorly developed. Phototropism is a big factor in directing growth into open places, where light is more abundant. Some plants,

hopelessly unable to outdo competitors in height, have become adapted to life in the shade and use the light with such economy that they are better off there than they would be in the sunshine. There is no doubt that in the struggle for existence some species have been so unadaptable to competition with their neighbors that they have either become extinct or been reduced to an inconspicuous place in the vegetation of the earth. Literally they failed to find their "place in the sun."

Review Questions

1. For what things do plants compete with each other?
2. In the competition for food, if one species is a rapidly growing one, by what means may its slow-growing rival be nourished?
3. What is the usual cause of injury in plants that are crowded?
4. Give a familiar example of the effects of competition for moisture.
5. In what ways may plants compete for light?

CHAPTER XXIX

ANIMAL DEPENDENCE ON PLANTS

All evidence points to the conclusion that plants and animals came from a common ancestor or a group of similar ancestors. For a time this primitive form of life could hardly have been classed as either plant or animal; it was too simple to have distinctive plant or animal characters. At a very early date, however, probably back in the Archeozoic era, some of these living things started on a course that led to the higher plants and others on a course that led to the higher animals. To reach these goals has required hundreds of millions of years, but consistently from the time of separation the two kingdoms appear to have remained distinct. What distinguishes plants from animals? There is no hard and fast rule. In general, plants have cellulose walls, contain chlorophyll, utilize the energy of sunlight and thus carry on photosynthesis, but do not ingest solid food. Animals, on the other hand, generally possess locomotion, have plastic, non-cellulose walls, lack chlorophyll, and are dependent on a supply of organic food which they ingest or swallow. If these rules are accepted there are plants that have at least one of the animal characters, and likewise there are animals that have one or more plant characters.

Origin of Animal Dependence.—It seems evident that animals from the beginning of their existence have depended upon plants for their food. Whether the first were saprophytes or parasites none can say, although parasitism seems to have been a later development. If we postulate that they have always been without chlorophyll, it follows that they had to find organic matter for food.

Locomotion among animals seems first to have been necessitated by a search for food, as warfare does not play a prominent part in the life of the lowest animals. Plants could anchor fast and let the sunlight come to them. Animals must go in search of food, except as it was accidentally brought to them by currents of water.

Animal Food at the Present Time.—We accept without question the fact that animals depend chiefly upon plants for food. Algae in the water; growing leaves, stems, and roots of higher plants; supplies of

stored food in seeds, bulbs, and tubers; the nectar and pollen of flowers —all these contribute heavily to the support of animal life. The *immediate* source of food may be other animals, but the *ultimate* source is plants.

This is necessarily so because animals lack the power of photosynthesis whereby plants obtain such vast supplies of energy from the sun and store it in the form of carbohydrates. They also lack the power that plants have of synthesizing proteins from the simplest food materials and have to reconstruct them from digested proteins already made. Most of the vitamins necessary for the normal development of higher animals are manufactured naturally only by plants although some have recently been synthesized. So while animals make a limited use of phosphates, iodides, and a few other inorganic substances their chief food supply comes directly or indirectly from plants. The mouths of animals have become highly specialized for securing different kinds of food, from soft juices to hard-shelled nuts. Preferential taste has been developed, especially among insects, some of which feed on one kind of plant and some on another. However, there are relatively few species of plants that are not relished by some kind of animal.

There is a remarkable instance of the artificial culture of plants for food by forms of animal life in the leaf-cutting ants of the tropics and sub-tropics of the western hemisphere. Of these there are five genera and nearly a hundred species. Their chief and almost sole food is a fungus grown on pulp made from fragments of leaves which the worker ants bring into their underground nests. With elaborate care the ants attend the fungus, preventing its fruiting and weeding out intruding fungi. When a young queen ant leaves the nest and establishes a new one, she takes a tiny pellet of the fungus with her and starts a new culture of it. The dependence of these leaf-cutting ants on this source of food has become absolute. The identification of this fungus is made difficult by the lack of fruiting bodies and the dearth of such fungi except under the care of the ants. There is some evidence that different species of ants grow different species of fungi.

It is surprising how few plants have evolved adequate defense mechanisms to protect themselves against animals. Some have developed sharp spines or stiff or stinging hairs, as the rose, the cactus, and the nettle; some have an unpleasant taste, as the mustards; and a few are poisonous, as the death camas. Devices for hiding seeds are found in the peanut and the Kenilworth ivy. For the most part, however, plants are defense-

less against animals, except as they may replace their lost parts with new ones, and it is fortunate that the larger animals generally feed over wide areas and rarely eat enough of any one plant to kill it outright.

Plant Uses Other Than for Food.—In this topic man will not be considered, for his uses of plants are so extensive that they become the basis of whole branches of agriculture, forestry, and medicine.

FIG. 293. Courting home of the orange-crested bower bird. (From J. Arthur Thomson's *New Natural History*, G. P. Putnam's Sons.)

Animals use plants to some extent for home building. Rodents drag grass into their holes for nests, but in this respect they are put to shame by the clever work of birds which use a great variety of materials and forms of architecture.

In the making of a temporary home the bower bird, of which there are several species, has gone far beyond simply building a nest. As a preliminary to mating, these birds construct elaborate rooms on the ground, using vines, branches, leaves, and twigs. They then gather from far and wide brilliantly colored objects—flowers, berries, shells, bones, broken glass, bright feathers, and anything that suits their gay fancy. With these they decorate the homes where they lead an enraptured life for a few days before flying away to rear their brood in a simple nest in a tree.

Honey bees inhabit hollow trees, sealing up the cracks with sticky material obtained from the buds of poplar and other trees. Certain social wasps, such as hornets and yellow jackets, make elaborate homes from wood pulp. Wood that is partly decayed or disintegrated by exposure to the weather is used after being macerated and mixed with saliva. A portion of this material is used to make a series of circular combs suspended horizontally one above another, supported by a central

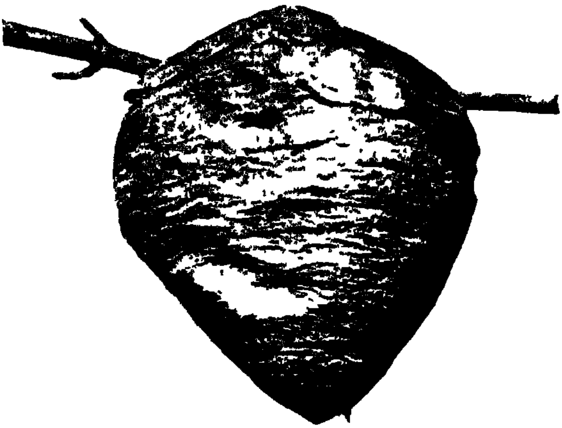


FIG. 294. Hornets' nest on the branch of a tree. About one-third natural size.

column and smaller vertical braces. In the cells of these combs the eggs are laid and the young are reared. With infinite care and skill the worker wasps use more of the wood pulp to construct about these combs layer after layer of paper wall, leaving an opening at the bottom. These walls serve to protect the insects from rain and cold. By actual test a temperature 30° F. higher inside than outside the nest has been recorded, the heat developed by the wasps being conserved to that extent. Leaf-cutting bees use discs which they rapidly cut with their mandibles from the leaves of rose, lilac, ash, and other plants to line their nests. These are preferably built in cylindrical holes, such as earthworm tunnels and the hollows of stems. Elliptical pieces are laid around the sides of the cylindrical space, and partitions are made and the ends are closed with circular discs. In the chambers arranged end to end in the cavity the young are reared, subsisting largely on honey that is deposited with the eggs.

The work of beavers in building dams and lodges of logs, sticks, etc., has been such a popular subject with writers that it needs no elaboration here. Of more widespread significance, but less discussed, is the value of forest shade and protection to birds and mammals.

FIG 295. Beaver lodge made of sticks and mud. The lodge rests on the bottom of the pond and the entrance is under water, but the living room is above the surface and is relatively dry. (Photograph by Wendell Chapman.)

It should be clear from these examples and others that could be cited that the varied use of plants by many animal species is greater than most people realize.

Books on natural history are rich in other examples of highly specialized uses of plants by animals. In these cases instinct has developed to a point where the cleverness of the animals has often been mistaken for reason.

It is doubtful if animals appreciate the beauty of the flowers, the grass, and the trees as we do, but the refuge of the forest has saved many of them from extermination.

REVIEW QUESTIONS

1. State the difference between the synthesis of proteins by plants and by animals.
2. What are the chief sources of energy for animals?

3. Explain why mammals seldom kill plants by eating them.
4. What group of animals does most serious damage to plants?
5. Name a benefit other than food that each of the following animals obtains from plants: (1) honey bees, (2) wasps, (3) rodents, (4) ants, (5) birds.
6. Cite a case of symbiosis between plants and animals.
7. How do wasps make paper for nest material?
8. How do leaf-cutter bees build nests in which to rear their young?
9. How does the new nest of the leaf-cutting ants become inoculated with the fungus used for food?
10. Why is it so difficult to determine the identity of the fungus grown for food by leaf-cutting ants?
11. What keeps the bits of wood from falling apart in a hornets' nest?
12. When beavers are making a dam in a wooded stream, why do the trees, when gnawed off, usually fall toward the water?

GLOSSARY OF TECHNICAL TERMS

The technical terms contained in this glossary are used in the text There are many other botanical terms which are not included Some of those listed here have more than one meaning, but in such cases only the meanings that apply to the subject of botany are given

Abscission layer. A region near the base of a petiole or a peduncle that disintegrates and thus provides for the normal shedding of the leaf or fruit

Achene. A small, dry, seed-like fruit Examples are furnished by the sunflower and the dandelion

Adaptive structures. Morphological structures that have come into existence through evolutionary processes and help to adapt the organism to environmental conditions

Adventitious. Growing in an unusual place For example, an adventitious root growing from a stem or a leaf, or an adventitious bud growing from a root, a leaf, or an internode

Aecidiospore. Same as aeciospore See footnote, page 298

Aecidium. Same as aecium See footnote page 298

Aeciospore. One kind of spore produced by a rust fungus, as in the stage of *Puccinia graminis* that is produced on the common barberry bush and attacks wheat and some grasses Same as aecidiospore

Aecium. The fruiting body of a rust fungus in the aecial stage Same as aecidium

Aerobic. Capable of using free oxygen for respiration

Agaricus. The generic name of certain mushrooms, including the kind most commonly grown for market

Aggregate fruit. A fleshy fruit formed from a flower with many separate pistils Example blackberry

Aleurone. The reserve protein material occurring as grains in a layer of cells near the outside of wheat and other cereals

Algae. The common name of a heterogeneous group of Thallophytes capable of carrying on photosynthesis and usually living in water Examples *Spirogyra, Oscillatoria,* and *Polysiphonia*

Allelomorph. Either one of a pair of contrasting characters transmitted from parent to offspring Example tallness or shortness

Ament. A kind of inflorescence containing apetalous, unisexual flowers arranged in a spike or a raceme Same as catkin Examples are found in willow, poplar, and birch

Ammonification. The production of ammonia from organic nitrogenous compounds such as proteins and urea.

Anabolism. Any chemical change taking place in the nutrition of a plant or animal by which simple materials are combined into more complex ones, with the storage of chemical energy. Example: photosynthesis.

Anaerobic. Incapable of using free oxygen in respiration but requiring oxygen in a combined form, such as sugar.

Analogous. Similar in appearance or function but not having the same origin. For example, the broad flat stems of the greenhouse smilax are analogous to leaves.

Anatomy. Internal structure, or the arrangement of tissues in a plant or animal.

Angiosperms. The class of seed plants characterized by the production of flowers and of fruits that enclose the seeds. Examples: apple and lily.

Annual. Completing the life cycle and dying within a year. The term is commonly applied to plants that produce seed and die the same season that they start from the seed. Examples: corn, tomato, and pumpkin.

Annual rings. Concentric layers of wood in dicotyledons and Gymnosperms. Normally a new one forms during each growing season.

Annulus. 1. A ring around the stipe of certain mushrooms which is the remains of the velum that was torn away as the stipe elongated and the pileus expanded. 2. A row of cells in the sporangium of a fern that aids in breaking the sporangium open and discharging the spores.

Anterior. The end that leads when an organism with locomotion moves about. The forward end.

Anther. A floral organ in which pollen grains are formed.

Antheridium. An organ in which male gametes are formed.

Antherozoid. A motile male gamete, or sperm.

Antipodal cells. In the embryo-sac within the ovule of a flower, the antipodal cells are those occupying the end opposite the egg.

Apetalous. Without petals. Descriptive of certain flowers such as those of box elder, willow, and buckwheat.

Archegonium. In Bryophytes, Pteridophytes, and Gymnosperms, the female organ that contains the egg.

Ascocarp. A structure that contains, and in some measure protects, an ascus or group of asci.

Ascomycetes. A large class of fungi characterized by a septate mycelium, absence of any motile stage, asexual spores usually formed by constriction, and typically eight ascospores formed in a sac by free cell formation. Example: *Sphaerotheca.*

Ascus. A sac in which eight spores (rarely four) are produced by free cell formation.

Autoecious. A term applied to rusts in which the life cycle is completed on one host plant.

Autophyte. A plant capable of manufacturing its own food from simple materials Examples algae, mosses, ferns, and most flowering plants, also a few species of bacteria.

Autotrophic. Capable of obtaining food and energy from inorganic substances

Auxiliary cells. In some red algae, cells that give their substance for the nourishment of the fertilized egg and its product

Auxin. A substance that promotes or regulates growth in plants A plant hormone.

Axil. The angle between a leaf and the stem above it

Azotobacter. A small genus of bacteria capable of fixing nitrogen without symbiosis with a higher plant

Bacillus. The generic name of certain rod-shaped bacteria

Bacteria. The common name for unicellular plants belonging to the class Schizomycetes

Basidiomycetes. A large class of fungi characterized by a septate mycelium, binucleate cells throughout most of the life cycle, and a club-shaped, spore-bearing organ—the basidium Examples mushrooms, rusts, and smuts

Basidiospore. One of a group of spores, usually four, borne on a basidium

Basidium. One of the club-shaped, spore-bearing organs of the Basidiomycetes, such as mushrooms

Bast fibers. Long, slender, thick-walled cells found in the phloem of many plants

Berry. A fleshy fruit formed from a single pistil and having several seed chambers but no papery core Examples cranberry and tomato

Biennial. Requiring approximately two years (commonly two summers and one winter) to complete the life cycle As a rule seeds are not produced until the close of the second season, after which the plants die Examples beet and carrot.

Blade. The expanded portion of a leaf

Bryophyta. The next to the lowest division of the plant kingdom, comprising the liverworts and mosses

Budding. A process of artificial propagation in which a bud cut from one plant is inserted under the bark of another plant and then grows out into a shoot. Used especially for peaches and other stone fruits.

Bulb. An organ of vegetative propagation consisting of the fleshy bases of leaves attached to a very short stem. Example: onion.

Callus. A mass of tissue that forms in a wound of a plant as it begins to heal.

Calyptra. A portion of a ruptured archegonium that forms a hood on the tip of a moss capsule.

Calyx. The outer whorl of floral leaves.

Cambium. A layer of embryonic cells such as that lying between the bark and the wood of a tree.

Capillitium. A mass of threads mingled with the spores in the fruiting bodies of most Myxomycetes and a few Basidiomycetes.

Capsule. 1. The sporangium of Bryophytes. 2. A dry, usually dehiscent fruit made up of several carpels. Examples: poppy, flax, and morning-glory.

Carbohydrate. A chemical substance composed of carbon, hydrogen, and oxygen, the last two in the proportion of two to one. Examples: sugars, starches, and cellulose.

Carpel. A specialized leaf that alone or in conjuction with others forms the pistil of a flower.

Carpogonium. The female reproductive organ in the red algae.

Carpospore. *One of the spores that form as a result of conjugation in* the red algae.

Caryopsis. The small, dry, seed-like fruit found in corn, wheat, and grasses.

Cast. A fossil formed by a deposit of minerals in a mold left by the dissolution of an organism or part from the space in which it was embedded.

Catabolism. Any chemical change taking place in the nutrition of a plant or animal, by which complex materials are broken down into simpler ones and chemical energy is released. Example: respiration.

Category. Any definite group into which plants or animals are divided for purposes of classification. Examples: class, family, and genus.

Catkin. A kind of inflorescence containing apetalous, unisexual flowers arranged in a spike or a raceme. Same as ament. Examples: willow, poplar, and birch.

Cell. A tiny mass of protoplasm enclosed within a plasma membrane; in plants usually bounded by a protective wall.

Cell plate. In a dividing cell of a higher plant, a protoplasmic layer formed across the cell by the spindle fibers that are left after the division of the nucleus. It later forms the plasma membranes against the new cell wall.

Cellulose. A carbohydrate substance that makes up a large part of the cell walls in most plants.

Chemical energy. The latent energy possessed by certain substances as a result of their composition. Carbohydrates and fats contain much chemical energy.

Chlamydomonas. The generic name of certain unicellular, flagellate, green algae.

Chlorophyceae. The class of plants to which the green algae belong.

Chlorophyll. The green pigments which aid in photosynthesis, and which are found in most plant cells.

Chloroplast. In the plant cell, an organ containing chlorophyll.

Chromatid. One of the four parts formed by the longitudinal splitting of homologous chromosomes during reduction division.

Chromatin. The material in a nucleus that transmits hereditary traits from parent to offspring.

Chromoplast. A plastid containing yellow pigments but little or no chlorophyll. Found in the petals of yellow flowers.

Chromosome. One of the units into which the spireme thread divides during mitosis.

Cilium. A whip-like, protoplasmic projection from the cell of certain lower organisms that serves as a means of locomotion.

Class. In plant classification, a group intermediate in rank between a division and an order.

Cleavage. A method of cell division in which furrows from the plasma membrane or from vacuoles divide a relatively large cell into smaller ones.

Clinostat. A piece of apparatus, usually run by clockwork, for slowly revolving a plant in any desired position.

Closed fibrovascular bundles. Fibrovascular bundles that have no cambium layer between phloem and xylem.

Coenocyte. The plant body of a Thallophyte consisting of one large cell with many nuclei.

Coleoptile. The sheath covering the plumule in the embryo of grains and grasses.

Colloid. This term was formerly used to designate a substance, such as gelatin, which, when mixed with water, would not diffuse through an osmotic membrane. It is now sometimes used for such a suspension of minute particles in water. More commonly the word colloid is avoided, and we speak of substances "in the colloidal state." In plants the most common forms of colloidal suspensions are a suspension of a solid in a liquid and a suspension of a liquid in a liquid, both found in cytoplasm. Elsewhere the colloidal state may include a liquid in a gas (fog), a solid in a gas (smoke), a

liquid in a liquid (an emulsion of oil in water), a solid in a liquid (water-glass), or a solid in a solid (the material in gall stones).

Companion cell. The sister cell of a sieve tube lying adjacent to it.

Compound leaf. One in which the blade is composed of separate leaflets. Examples: clover and walnut.

Conceptacle. A pit in the thallus of a brown alga, such as *Fucus*, containing antheridia or oogonia.

Cone. A collection of spore-bearing scales attached to a central axis. Same as strobilus.

Conidiophore. A specialized hypha that produces spores at its tip by constriction.

Conidium. A spore cut off from the tip of a conidiophore by constriction.

Conjugation. The intimate union of two gamete cells to form a zygote.

Corm. A fleshy underground stem bearing roots at the base and serving as a means of natural vegetative propagation. Example: *Gladiolus*.

Corolla. The whorl of floral leaves, usually showy, borne just inside the calyx.

Cortex. The region of a stem or a root between the epidermis and the stele.

Corymb. An inflorescence in which the flower stalks are attached to a central rachis, and the lower ones bearing the older flowers are longer than the upper ones bearing the younger flowers. Examples: apple and *Spirea*.

Cotyledon. One of the first leaves of an embryo plant, usually forming a conspicuous part of the seed.

Cupule. A small, cup-shaped receptacle found on the thallus of some liverworts and containing gemmae.

Cuticle. The outer layer of the outside wall of epidermal cells.

Cyanophyceae. The class of Thallophytes to which the blue-green algae belong.

Cyme. An inflorescence in which the central, terminal flowers open before the outer, lower ones. They are produced by the wild geranium, some species of St. John's-wort, and a limited number of other plants.

Cystocarp. A receptacle or sheath enclosing the carpospores in *Polysiphonia* and some other red algae.

Cytology. That branch of biological science that deals with the structure and physiology of cells.

Cytoplasm. That portion of the protoplasm in which the other cell organs—nucleus, plastids, etc.—are suspended.

Deciduous. Descriptive of plants that shed their leaves at the close of the growing season.

Dehiscent. Descriptive of fruits that open naturally and thus release their seeds. Examples: columbine and poppy.

Dialysable. Capable of being separated by osmosis. For example, a protein can be freed from a sugar by placing the mixture in a membranous sac which is then suspended in water.

Diatom. A unicellular alga possessed of a hard, silicious wall in the form of a box.

Dichotomous branching. Dividing into two branches approximately equal in size.

Dicotyledons. A sub-class of flowering plants having two seed leaves. Examples: bean and squash.

Diffusion. Spreading about or dispersing by means of molecular activity.

Dihybrid. The result of a cross between parents that differ in two heritable characters.

Dioecious. Producing male organs on one individual and female organs on a different individual. Same as unisexual. Examples: *Marchantia* and willow.

Diploid. The greater of the two numbers of chromosomes occurring in the nuclei during different phases of the life cycle of most plants. The chromosome number of the sporophytic phase or generation.

Division. Any one of the four great groups that make up the plant kingdom; for example, all of the seed plants.

Dominant. A character that appears in the first generation following the cross breeding of parents unlike with respect to that character. For example, in peas smoothness is dominant over roughness in the seeds.

Drupe. A fleshy fruit containing a central pit or stone. Examples: peach and cherry.

Ecology. That branch of biological science that treats of the relations of living things to their environment.

Elaters. The thread-like cells that aid in the expulsion of spores from the sporangia of certain Bryophytes and Pteridophytes.

Elodea. The generic name of a small, aquatic, flowering plant, the leaves of which are commonly used for a study of cells in their living condition.

Embryo. In botany, a very young sporophytic plant such as that found in a seed.

Embryonic cells. Undifferentiated cells that divide at frequent intervals. They are commonly found in growing-points and in the cambium layer.

Embryonic regions. Regions where embryonic cells are found, such as the cambium layer and the growing-points of roots and shoots.

Endodermis. The innermost layer of cells in the cortex.

Endosperm. In a seed, the food storage region outside the embryo.

Entire leaves. Leaves with smooth margins, i.e., not notched or cleft.

Epicotyl. The internode of a seedling plant between the node bearing the cotyledons and the plumule above.

Epidermis. The outer layer of cells covering a plant.

Epiplasm. Cytoplasm that is not included within the ascospores in an ascus but fills the space between them.

Equisetum. The generic name of Pteridophytic plants commonly called horsetails or scouring-rushes.

Etiolated. Bleached or whitened, as in the case of a plant that has been kept away from the light.

Euglena. The generic name of certain unicellular, flagellate organisms.

Evergreen. Retaining green leaves throughout the winter. Examples: pine and holly.

Evolution. The progressive development of one thing from another. Commonly applied to the origin of one species from another by progressive changes.

Factor. In genetics a factor is a gene or a combination of genes that serves to transmit a given trait from parent to offspring.

Family. In plant classification, a group intermediate in rank between a tribe and an order.

Fascicled. Arranged in a cluster, the individuals usually being approximately equal in size.

Fibrovascular bundles. Collections of cells that make up the stele and extend from the roots to the leaves.

Filament. A thin strand or thread. In many Thallophyta the body of the plant is a filament made up of a single row of cells attached end to end.

Fission. Cell division by constriction, if the two daughter cells are equal in size.

Flagellata. A class of unicellular organisms that swim about by means of one or two polar flagella. As a group they show some animal and some plant characters.

Flagellum. A whip-like, protoplasmic projection from the cell of certain lower organisms, that serves as a means of locomotion.

Fossil. The remains or imprint of a plant or an animal preserved in rock.

Free cell formation. The method of cell division by which ascospores are produced in an ascus.

Fucoxanthin. A brown pigment found in the cells of brown algae.

Fucus. The generic name of certain brown algae.

Funaria. The generic name of certain mosses.

Fungi. The common name of a heterogeneous group of Thallophytes having a filamentous structure and no chlorophyll. The plural form of fungus.

Fungi imperfecti. Fungi in which the sexual method of reproduction has been lost through degeneration.

Fungus. The singular form of fungi.

Gametangium. A reproductive organ in which one or more gametes are produced.

Gamete. Either of the two cells that unite in sexual reproduction.

Gametophore. A stalk on which a gamete is produced.

Gamopetalous. Descriptive of flowers in which the petals are united to each other, as in morning-glory and squash. Same as sympetalous.

Gemmae. The tiny buds that form in the cupules of certain liverworts and develop into new plants.

Gene. In a nucleus, a minute body which, individually or in conjunction with other genes, transmits a hereditary trait from parent to offspring.

Genus. In plant classification, a group intermediate in rank between a tribe and a species.

Geotropism. The tendency of plant parts to respond to the stimulus of gravity.

Glycogen. A carbohydrate material similar to starch.

Gradient. A condition existing between two regions that differ in the concentration of a substance, such as sugar, in which the concentration is progressively increasing or decreasing from one to the other as the material diffuses.

Grafting. A process of artificial propagation in which a portion of a shoot of one plant is inserted into an opening made in another, after which the buds of the scion grow out into shoots.

Guard cells. A pair of special epidermal cells bounding a stoma.

Gymnosperms. The class of seed plants in which the ovules are not enclosed within carpels. Examples: pine, fir, hemlock, and larch.

Halophytes. Plants that thrive in soils that are relatively high in chlorides and other inorganic salts.

Haploid. The lesser of the two numbers of chromosomes occurring in the nuclei during different phases of the life cycle of most plants. The chromosome number of the gametophytic phase or generation.

Haustorium. 1. In certain parasitic fungi, a special hypha that enters the host cell and absorbs nourishment from it. 2. In parasitic

flowering plants an organ analogous to that in parasitic fungi, by which nourishment is taken from the host.

Head. A kind of inflorescence in which flowers that are sessile or nearly so are attached at practically the same point. Found in sunflower and other composites, in sycamore, and in a number of other plants.

Heart-wood. The older wood in a tree, usually dark in color and no longer capable of conducting sap.

Heliotropism. The tendency of plant parts to respond to the stimulus of light. Same as phototropism.

Hepaticae. The class of Bryophyta to which the liverworts belong.

Herbaceous. Having stems relatively soft in texture and dying to the ground in the fall, if growing in regions with cold winters.

Heterocyst. One of the large, yellowish cells in the filaments of certain blue-green algae.

Heteroecious. A term applied to rusts in which more than one species of host plant is required for the completion of the life cycle.

Heterogametes. Gametes that differ morphologically from each other, usually consisting of large female and smaller male that are motile in some species.

Heterospory. The production of two or more different kinds of spores.

Heterothallic. Among the lower plants, production of only one kind of gamete by the same plant. Equivalent to dioecious.

Heterozygous. Descriptive of individual plants in which the nuclei of the sporophyte contain opposite factors for a given unit character.

Homologous. In plant morphology structures are called homologous if they have the same origin. For example, the thorns of the black locust are homologous with stipules.

Homologous chromosomes. A chromosome pair, one from a male gamete and the other from a female gamete, both bearing genes relating to the same hereditary characters.

Homospory. The production of only one kind of spore.

Homothallic. Among the lower plants, producing both male and female gametes on the same plant. Same as monoecious.

Homozygous. Descriptive of individual plants in which the nuclei of the sporophyte contain like factors for a given unit character.

Hormone. A substance that promotes or regulates growth.

Humus. Organic matter in the soil, which has disintegrated to the point where its original structure is no longer recognizable.

Hydathode. A water pore, usually at the end of a vein in the margin of a leaf, capable of exuding water in the liquid state.

Hydrophytes. Plants adapted for growth in water or in very wet places. Examples: *Elodea* and water-lilies.

Hypha. A branch of a fungus mycelium.

Hypocotyl. That portion of the stem of a seedling plant that is between the point of attachment of the cotyledons and the root system.

Imbibition. The absorption of water by organic matter into parts that show no visible spaces.

Imperfect flower. A flower that lacks either stamens or pistils.

Inclusion. A method of fossilization in which the embedding material hardens about the organism or part.

Indehiscent. Descriptive of a fruit not opening naturally to release the seeds. Examples: acorn, peanut, and sunflower.

Infiltration. A method of fossilization in which a dead plant or animal is penetrated by minerals in solution.

Inflorescence. A natural cluster of flowers on a plant. Examples: head of sunflower, umbel of parsnip, and spike of plantain.

Integument. One or two layers of tissue that start around the base of an ovule and grow until they cover it except for the micropyle. Later they become the seed coats.

Intercalary. Growth in the region between the tip and the base.

Intercellular spaces. Spaces between cells, usually containing air.

Internode. The portion of a stem between the nodes.

Intramolecular respiration. A kind of respiration in which the oxygen is obtained from a compound, such as sugar, rather than in the free state. Same as anaerobic respiration.

Irritability. The sensitivity of a plant or an animal to a stimulus, such as light or gravity.

Isogametes. Gametes that are morphologically alike.

Latex. The milky juice occurring in many plants, such as lettuce, dandelion, and rubber trees.

Layering. A method of artificial propagation in which a branch is bent down and covered with soil until it establishes a root system of its own. Used for woodbine, grape, and some shrubs.

Leaf scar. The scar left on a stem where a leaf has dropped off.

Leaflet. One of the parts that make up the blade in a compound leaf, such as clover and woodbine.

Legume. 1. A plant belonging to the pea family. 2. The pod of a plant belonging to this family.

Lenticel. One of the numerous, tiny, spongy regions in the young bark of many trees and shrubs, through which the tissues are aerated.

Leucoplast. A plastid that is white or transparent from lack of pigment.

Lichen. A combination of fungus and alga intimately associated and having the appearance of an individual plant.

Linin thread. In a nucleus, a network of material that connects the chromatin particles with each other.

Liverwort. A simple green plant belonging to the class Hepaticae and closely related to the mosses. Example: *Marchantia.*

Lycopod. A Pteridophytic plant commonly called a club-moss.

Marchantia. The generic name of a highly specialized liverwort.

Mastigophora. A class of lower organisms having some plant characters and some animal characters. Another name for the Flagellata.

Maturation. The change from the sporophytic to the gametophytic phase, which is accompanied by a reduction in the chromosome number from the diploid to the haploid.

Medullary rays. Plate-like extensions of the pith between the fibrovascular bundles of many plants. Not to be confused with xylem rays that occupy a similar position.

Megaspore. The larger of the two kinds of spores in heterosporous plants.

Meiosis. Maturation divisions in a spore mother cell, resulting in a reduction of chromosome number from the diploid to the haploid.

Meristem. A region in which extensive cell division is normally taking place. An embryonic region.

Mesophyll. The palisade layer and the spongy layer of parenchyma in a leaf taken collectively.

Mesophytes. Plants adapted to growth in soils of moderate water content.

Metabolism. Any chemical change that takes place within a plant or animal with reference to its nutrition. For example, respiration and photosynthesis.

Micron. One one-thousandth of a millimeter.

Micropyle. The opening in the covering of an ovule through which the pollen tube enters.

Microspore. The smaller of the two kinds of spores in heterosporous plants.

Midrib. The main vein running lengthwise through many kinds of leaves, such as those of apple and willow.

Monocotyledons. A sub-class of flowering plants having only one seed leaf. Examples: lily and corn.

Monoecious. Bearing both staminate and pistillate flowers on the same individual. Example: corn.

Monohybrid. The result of a cross between parents that differ with respect to a single heritable character.

Morel. A fleshy fungus belonging to the class Ascomycetes.

Morphology. The study of the form and structure of plants and animals.

Moss. A flowerless plant belonging to the division Bryophyta and class Musci.

Multiple fruit. A fleshy fruit developed from a short spike or other inflorescence, the entire inflorescence forming one fruit. Examples: mulberry and fig.

Musci. The class of plants to which the mosses belong.

Mutation. The radical departure of an offspring from certain parental characters.

Mycelium. The mass of threads that make up the body of a fungus.

Myxamoeba. A naked, ameboid cell that comes from the germinating spore of a slime mold.

Myxomycetes. A class of low, chlorophylless plants, in which the vegetative state is a naked, multinucleate plasmodium.

Nemalion. The generic name of certain red algae.

Nitrification. A process by which ammonium compounds in the soil are changed to nitrates through the action of certain bacteria.

Nitrogen fixation. The combining of the free nitrogen of the air into nitrogenous compounds. One method is through the activities of certain bacteria in the soil or in the roots of leguminous plants.

Node. The region of a stem that normally produces leaves and buds.

Nodule. Bacterial galls on the roots of leguminous plants.

Nomenclature. In botany, the science of naming plants.

Nostoc. The generic name of certain kinds of blue-green algae.

Nucellus. The tissue of an ovule within which the megaspore forms and develops into a female gametophyte.

Nucleolus. A lump of reserve material in the nucleus.

Nucleus. A body in the cell that controls certain of its activities, including the transmission of hereditary traits.

Nut. A hard, dry fruit larger than an achene. Examples: acorn and filbert.

Nutation. The circular motion of growing stems; apparently not initiated by external stimuli.

Oogonium. A specialized cell in which one or more female gametes are formed.

Oomycetes. A small sub-class of fungi characterized by a non-septate mycelium and the production of zoospores. Examples: *Saprolegnia* and *Phytophthora*.

Oospore. A sexually formed spore produced by the union of a small male and a large female gamete.

Open fibrovascular bundles. Fibrovascular bundles that have a cambium layer between phloem and xylem.

Operculum. A cap or lid at the tip of the capsule of a moss.

Order. In plant classification, a group intermediate between a class and a family.

Orthogenesis. A theory which proposes that when variation starts in a certain direction it will continue and accumulate through generation after generation.

Oscillatoria. The generic name of certain filamentous blue-green algae.

Osmosis. The diffusion of substances through a membrane.

Ovary. The basal portion of the pistil of a flower.

Ovule. A small body that develops into a seed.

Palisade layer. A layer of elongated cells containing many chloroplasts. It occupies the upper portion of the leaf, just beneath the epidermis.

Palmate. A kind of compounding of leaves in which the leaflets are attached at approximately the same point at the top of the leaf stalk. Examples: clover, woodbine, and lupine.

Panicle. An inflorescence in which there is repeated branching, each branch bearing a flower. Example: lilac.

Parasite. An organism that lives on or in a plant or animal of a different species and takes nourishment from it.

Parenchyma. A tissue composed of large thin-walled cells. Example: pith.

Parthenogenesis. The development of an unfertilized egg into an individual.

Pedicel. The stalk of each flower in an inflorescence.

Peduncle. The stalk of a solitary flower. Compare with pedicel.

Pericycle. The outermost layer of the stele—usually consisting of one layer of cells but sometimes more.

Pepo. The fruit of the squash and other members of the same family.

Perennial. A plant that continues to live for several or many years.

Peristome. A fringe of flexible teeth around the opening in the capsule of a moss.

Perithecium. A small, spherical, or flask-shaped ascocarp. Examples are found in the powdery mildews such as *Sphaerotheca*.

Petal. One of the floral leaves that collectively make up the corolla of a flower.

Petiole. The stalk of a leaf.

Petrified. Changed to stone. Descriptive of wood that has been fossilized by infiltration with silica or lime.

Phaeophyceae. The brown algae. A class of marine algae, some of very great size. Examples: *Ectocarpus, Fucus,* and *Macrocystis.*

Phloem. The portion of the fibrovascular system that is composed of sieve tubes, companion cells, and sometimes bast fibers. In most higher plants it is the portion of the stele that lies outside the cambium layer.

Phototropism. The tendency of plant parts to respond to the stimulus of light. Same as heliotropism.

Phycocyanin. The blue pigment in the cells of the Cyanophyceae.

Phycoerythrin. The red pigment in the cells of the Rhodophyceae.

Phycomycetes. A small class of fungi characterized by a non-septate mycelium. Examples: *Rhizopus* and *Saprolegnia*.

Physiology. That branch of biology that deals with functions such as nutrition, locomotion, and reproduction.

Phytophthora. The generic name of the fungus that causes late blight of potatoes.

Pileus. The expanded portion, or cap, at the top of a mushroom.

Pinnate. A kind of compounding of leaves in which the leaflets are attached at different points along a rachis. Examples are found in Boston fern, walnut, and ash.

Pistil. The central organ of a flower, composed of one or more carpels, which develops into the fruit enclosing the seeds.

Pistillate flower. A unisexual flower having pistils but no stamens.

Pith. The central portion of the stem in many dicotyledonous plants.

Plasma membrane. The outer layer of protoplasm in a cell.

Plasmodium. A naked, multinucleate cell constituting the vegetative stage in a Myxomycete.

Plasmolysis. The collapse of a cell due to loss of water through osmosis.

Plastid. One of the small, dense bodies in a cell. In the presence of light they usually develop pigments—green, yellow, etc.

Plume. A light, hairy or feathery appendage on an achene or a seed, which aids in wind distribution. Examples: dandelion and fireweed.

Plumule. The first bud on the embryonic plant in a seed.

Pod. A dry fruit of one carpel containing several to many seeds. Examples: pea and bean.

Polar cap. One of the two aggregations of material that form the spindle fibers in mitotic division of the nucleus.

Pollen. Small grains that form in the anthers of flowers. They start as microspores and develop into male gametophytes.

Pollination. The transfer of pollen from anther to stigma.

Polypetalous. Descriptive of flowers that have petals distinct from each other. Examples: apple, rose, and St. John's-wort.

Polypodium. The generic name of certain ferns.

Polysiphonia. The generic name of certain red algae.

Pome. A fleshy fruit containing several seed chambers inside a papery core. Example: apple.

Posterior. The rear end as contrasted with the anterior or forward end.

Primordium. The rudimentary structure that develops into an organ such as a leaf or a bud.

Promycelium. In rust fungi, the basidium which grows from a cell of the teliospore in germination.

Prop roots. Aerial roots that grow into the ground and thus support the stem. Examples are found in corn, some palms, and some figs.

Prothallium. The small thallus that makes up the gametophyte of a fern or other Pteridophyte.

Protococcus. The generic name of certain unicellular green algae.

Protonema. The alga-like structure produced by the germinating spore of a moss.

Protoplasm. The living material in a cell.

Protoplast. The cell exclusive of the cell wall.

Pteridophyta. A division of the plant kingdom that includes the ferns, club-mosses, and horsetails.

Puccinia. The generic name of certain rust fungi.

Pulvinus. The swollen basal portion of the petiole in the sensitive-plant and some others.

Pycniospore. One of the spore-like cells of rusts that appear to function as male gametes. Same as spermatium.

Pycnium. The receptacle in a rust in which pycniospores are produced. Same as spermogonium.

Pyrenoid. In certain algae, a refractive, starch-forming body surrounded by chlorophyll.

Raceme. An indeterminate inflorescence consisting of a central stalk to which the flowers are attached by unbranched pedicels. Examples: shepherd's purse, lupine, and chokecherry.

Rachis. 1. In a compound leaf, the extension of the petiole to which the leaflets are attached. 2. In an inflorescence such as a spike, the central stalk to which the pedicels are attached.

Radicle. The root of the embryo in a seed.

Receptacle. In a flower, the end of the peduncle to which the floral leaves are attached.

Recessive. A character that fails to appear in the first generation following the cross-breeding of parents unlike with respect to that character. For example, in peas, roughness of the seed is recessive when contrasted with smoothness of the seed.

Regeneration. A process in which a new part grows and replaces an old one that has been lost.

Respiration. The oxidation of suitable carbonaceous materials in plants and animals with the formation of carbon dioxide and the release of chemical energy.

Rhizobium. The generic name of certain bacterial organisms that can carry on nitrogen fixation in symbiosis with leguminous plants.

Rhizoids. In the lower plants, branches that function as roots in that they anchor the plant and, in some cases, absorb water and food.

Rhizome. A slender, underground stem that aids in natural vegetative propagation. Same as rootstock. Examples are found in quack grass and the "stem" of a potato tuber.

Rhizopus. The generic name of a fungus commonly called bread mold.

Rhodophyceae. The class name of the red algae.

Root-cap. A mass of cells that protects the growing tip of a root.

Root-hairs. Slender extensions of the epidermal cells of roots, that function in the absorption of water and mineral food from the soil.

Root pressure. Pressure developed by osmosis in the roots, which aids in the ascent of sap.

Rootstock. Same as rhizome.

Runner. Same as stolon.

Saccharomyces. The generic name of certain kinds of yeast plants, including those used for alcoholic fermentation and bread raising.

Saprolegnia. The generic name of certain Phycomycetes that live on organic matter in water.

Saprophyte. An organism that obtains its food from non-living organic matter.

Sap-wood. The outer, light-colored portion of the wood of many trees. The part that conducts sap up the stem.

Schizomycetes. The class name of the group to which the bacteria belong.

Scion. A portion of one plant (usually a piece cut from a stem) that is inserted into another plant, the stock, in grafting.

Sclerenchyma. A tissue composed of thick-walled cells. Found in the shells of nuts, in wood and bark, and in many other places.

Seed. The embryo of a higher plant, together with its enveloping seed coats and stored food.

Selaginella. The generic name of a group of the Pteridophytes.

Sepal. One of the outer whorl of floral leaves that cover the more central parts in the bud.

Septum. In fungi, a cross-wall in a hypha.

Sessile. Attached directly without a stalk, as are the leaf blades of many kinds of plants and the flowers in a spike.

Seta. The stalk bearing the capsule in a moss or a liverwort.

Sheath. The basal part of a leaf that surrounds and is attached to the stem in corn and other grains and grasses.

Sieve plates. Small perforated areas in the walls of sieve tubes; usually the cross-walls separating one sieve tube from the adjoining one above or below.

Sieve tubes. Cells in the phloem that conduct foods.

Simple leaf. One in which the blade is composed of a single part rather than of leaflets. Examples: lilac and sunflower.

Slime mold. The common name for a member of the Myxomycetes.

Solute. A substance that is dissolved in a solvent.

Soredium. A minute body consisting of a little of the alga and of the fungus from a lichen and serving to propagate it by growing into a new lichen.

Spadix. A kind of inflorescence consisting of a spike, the upper portion of which bears staminate flowers and the lower portion pistillate flowers. Examples: calla-lily and cat-tail.

Spathe. A special leaf, often showy in appearance, that encloses a spadix from below. For example, the conspicuous white portion of a calla-lily.

Species. A group of plants or animals including all the individuals that are essentially alike.

Sperm. A male gamete, particularly a motile male gamete.

Spermatium. The sex cells produced within a spermogonium. Synonymous with pycniospore in rusts. See footnote page 298.

Spermatophyta. The division of plants comprising those that produce seeds.

Spermogonium. In a rust fungus, the container in which the spermatia are produced. Same as pycnium.

Sphaerotheca. The generic name of certain of the powdery mildews.

Sphagnum. The generic name of certain mosses extensively used for packing plants for shipment.

Spike. An inflorescence consisting of a central stalk or rachis to which are attached sessile flowers. Example: plantain.

Spindle fibers. Protoplasmic strands that take part in mitosis.

Spireme thread. A strand made up of the chromosomes connected end to end in early stages of mitosis.

Spirillum. The generic name of certain bacteria that have the shape of spiral rods.

Spirogyra. The generic name of certain green algae with unbranched filaments and chloroplasts in the form of spiral bands.

Spongy layer. The portion of the mesophyll of a leaf that lies between the palisade layer and the lower epidermis and has large intercellular spaces.

Sporangiophore. A stalk that bears one or more sporangia.

Sporangium. A sac or container in which spores are produced.

Spore. A simple reproductive body made up of one, or very few, cells.

Sporidium. In the rust and smut fungi, a basidiospore or other one-celled spore that is thin-walled and usually colorless.

Sporophore. A stalk that produces a spore at its tip by constriction.

Sporophyll. A leaf that is specialized for the production of spores, as a stamen or a carpel.

Stamen. One of the floral organs that produce pollen grains.

Staminate flower. A unisexual flower having stamens but no pistils.

Stele. In Pteridophytes and Spermatophytes, the central region of stems and roots, occupied by the fibrovascular system

Sterigma. One of the stalks that project from a basidium and bear basidiospores.

Stigma. The usually expanded tip of a pistil suited to the catching and germinating of pollen grains

Stipe. The stalk of a mushroom

Stipules. One of the pair of scale-like portions of a leaf borne at the base of the petiole.

Stock. The plant or part of a plant in which the scion is inserted in grafting.

Stolon. 1 A slender stem that extends laterally from a plant and takes root, thus aiding in vegetative propagation Example: strawberry 2 A hypha that extends outward from the main body of a fungus, as in *Rhizopus*

Stoma. An opening in the epidermis through which gas exchange takes place between the plant and the air.

Streptococcus. The generic name of certain bacteria that are spherical in shape and produced in chains.

Strobilus. A collection of spore-bearing scales attached to a central axis. Same as cone

Style. The portion of the pistil of a flower between the ovary and the stigma.

Suspensor. In *Rhizopus* and its relatives, one of the pair of gametophores attached to the zygospore

Symbiont. Either of two unrelated organisms that live in intimate association and mutually benefit each other, as fungus and alga in a lichen.

Symbiosis. A relationship between organisms of two different species in which there is mutual benefit derived from the association Illustrated by lichens and by bacteria of the genus *Rhizobium* in the nodules of leguminous plants.

Sympetalous. Descriptive of flowers in which the petals are united to each other, as in morning-glory and squash. Same as gamopetalous.

Synergids. The two cells associated with the egg in the embryo sac.

Teleology. The erroneous idea that organic adaptation is explained by purpose rather than by inheritance and environment.

Teleutospore. Same as teliospore. See footnote, page 298.

Teliospore. A spore of the black, or winter, stage of a rust fungus. Same as teleutospore. See footnote, page 298.

Telium. A mass of black rust spores borne in a pustule on a host plant. Same as teleutosorus.

Terrestrial. In botany, growing on land as contrasted with growing submerged in water.

Tetraspore. In the Rhodophyceae, one of the four spores formed by two successive divisions of a spore mother cell and beginning the gametophyte generation.

Thallophyta. The lowest division of the plant kingdom, including the algae and the fungi.

Thallus. The gametophytic vegetative part, or body, of the lower plants.

Thigmotropism. The tendency of plant parts to respond to the stimulus of touch.

Translocation. The transport of plant food from one part of a plant to another.

Transpiration. The loss of water by a plant in the form of water vapor, chiefly through the stomata.

Tribe. In plant classification, a group intermediate between a family and a genus.

Trichogyne. An extension of the oogonium in certain Rhodophyceae and Ascomycetes.

Truffle. A roundish, fleshy, ascomycetous fungus that develops underground.

Tyloses. Bladder-like protrusions from wood parenchyma cells into the xylem vessels of some woody plants.

Ulothrix. The generic name of certain green algae.

Umbel. An inflorescence in which the pedicels of the flowers are attached at practically the same point at the tip of a stem.

Unit character. In genetics, any character inherited independently of other characters except through linkage.

Urediniospore. A spore of the red, or summer, stage of a rust. Same as uredospore. See footnote, page 298.

Uredinium. A mass of red rust spores borne in a pustule on a host plant. Same as uredosorus.

Uredospore. Same as urediniospore. See footnote, page 298.

Ustilago. The generic name of certain smut fungi.

Vacuole. A space in the cytoplasm of a cell, filled with non-protoplasmic liquid, chiefly water and mineral salts.

Vascular bundles. Bundles of xylem and phloem cells that make up the stele.

Vaucheria. The generic name of certain green algae.

Veins. The fibrovascular bundles in a leaf.

Velum. In young mushrooms, a delicate membrane extending from the stipe to the margin of the pileus.

Venation. The course of the veins through the blade of a leaf.

Water pore. An opening, usually at the end of a leaf vein, from which water in the liquid state exudes. Same as hydathode.

Whorled. Arranged in a circle, as a whorl of leaves around a stem.

Wing. On an achene or a seed, a flat, thin appendage that aids in wind distribution. Examples: maple and pine.

Woody. Descriptive of tissues that are hard from the presence of lignin in the cell walls.

Xerophytes. Plants adapted to life in dry places, such as deserts. Examples: cactus and Spanish bayonet (*Yucca*).

Xylem. The woody portion of the stele. In most dicotyledonous plants and Gymnosperms, all the region inside the cambium layer, exclusive of the pith.

Yucca. The generic name of certain desert plants, including the Spanish bayonet and the "Joshua palm."

Zoosporangium. A cell in which zoospores form.

Zoospore. A motile spore. Same as swarm spore.

Zygomycetes. A sub-class of the Phycomycetes that contains *Rhizopus* and related molds.

SINGULAR AND PLURAL FORMS OF BOTANICAL TERMS HAVING LATIN OR GREEK ENDINGS

Alga—algae
Antheridium—antheridia
Archegonium—archegonia
Ascus—asci
Bacterium—bacteria
Basidium—basidia
Cilium—cilia
Conidium—conidia
Flagellum—flagella
Fungus—fungi
Gemma—gemmae
Genus—genera
Haustorium—haustoria
Hypha—hyphae
Mycelium—mycelia
Nucleus—nuclei
Oogonium—oogonia
Perithecium—perithecia
Primordium—primordia
Prothallium—prothallia
Protonema—protonemata
Septum—septa
Sorus—sori
Species—species
Sporangium—sporangia
Sporidium—sporidia
Sterigma—sterigmata
Stimulus—stimuli
Strobilus—strobili
Thallus—thalli

INDEX

(Pages bearing illustrations are in bold-face type.)